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Production in Coastal Salt Marshes of Southern California

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by

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ABSTRACT

Production ecology in southern California coastal salt marshes was investigated by harvesting macrophytes and monitoring environmental factors (substrate salinity, pH, nitrogen, redox, water content, temperature, and tide level) at four locations--Sweetwater River Estuary, Los Penasquitos Lagoon, Upper Newport Bay, and Bolsa Bay--over an annual cycle beginning fall 1977. Net aerial primary production estimates computed by summing production in individual species and adjusting for interval death and shedding and disappearance of dead material averaged 3196, 3787, 2150, and 2494 g $m^{-2}yr^{-1}$ for study sites, and were 1.3 to 1.7 times greater than estimates computed by the method of Smalley (1959). Instantaneous rates of disappearance for dead material based on litter bag sets ranged from 2.2 to 2.7 mg g^{-1} day^{-1} and were lowest at Los Penasquitos Lagoon. Production levels were highest on creek levees and transition to upland and lowest in back levee depressions, fore levee slopes, and pans--suggesting that habitat, especially drainage and salinity, exerts greater control over macrophyte production in the marsh than does tide level alone. High levels of production in Salicornia virginica and Frankenia grandiflora at Los Penasquitos Lagoon suggests that production in some plant species may be increased by reduced tidal contact.

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INTRODUCTION

Purpose and Scope

This study was designed to answer four questions about macrophyte production in coastal salt marshes of southern California: a) what levels of production are achieved by plant species and plant communities; b) to what extent does production vary within and between marshes especially those with and without regular tidal inundation; c) what physical factors control or best explain variations in production; and d) how does production in southern California salt marshes compare with that at other latitudes on the Pacific Coast and at similar latitudes on the Atlantic Coast?

Salt Marshes and Production

A growing literature suggests that coastal salt marshes are among the most productive of natural systems (Teal 1962, Cooper 1974, Clark 1974, Chapman 1976, Turner 1976). Salt marshes occupy a fortunate position between the limits of tidal inundation. Essential nutrients entrained by terrestrial runoff are transported along with nutrients from coastal waters to marsh soils by tidal flux (Steever et al. 1976). While primary production in the marsh is high, marked variations in yield occur. Explanations for intramarsh variations in production, and species distribution as well, have involved factors related to tides; such as, frequency and duration of tidal inudation (Mahall 1974, Eilers 1975, Mahall and Park 1976c), tidal range (Steever et al. 1976), waterlogging (Brereton 1971), drainage density and proximity to creek channels (Smalley 1959, Eilers 1975), and soil salinity (Adams 1963, Good 1972, Mahall and Park 1976b). Several authors (Tyler 1967, Valiela and Teal 1974, Patrick and Delaune 1976) have demonstrated the importance of soil nitrogen (especially ammonia) to the level of production, and others (Adams 1963, Tyler 1971) have shown that species occurrence as well as yield may be related to the abundance of soil iron.

Production by salt marsh autotrophs is only partially consumed by in situ herbivory (Smalley 1959, Teal 1962). Much of the remaining dead leaves and stems of marsh macrophytes are acted upon by bacteria and transported from the marsh by tides as energy and nutrient-rich organic detritus (Odum and de la Cruz 1967). This material becomes an important food source for estuarine consumers, expecially filter feeders, and thereby aids in the maintenance of the high level of secondary production characteristic of coastal ecosystems. Export of particulate detritus is greatest for intertidal elevations in the marsh and decreases with declining inundation frequency (de la Cruz 1973, Eilers 1975, Heinle and Flemer 1976). In situ decomposition in the high marsh is likely to be more complete due to the rarity of tidal inundation and,

therefore, export materials from more elevated positions take the form of soluble organics and nutrient ions which are carried seaward by rainfall and extreme high tides.

Knowledge of marsh production in North American and its influence on general coastal productivity rests almost totally on investigations conducted along the Atlantic and Gulf Coasts. While much of the value placed on Eastern marshes has been applied to those of the West Coast by such agencies as the California Coastal Zone Conservation Commission (CCZCC 1975) and the San Francisco Bay Conservation and Development Commission (SFBCDC 1969), the productivity of Pacific marshes, especially those along the California coast, has yet to be fully demonstrated. Turner (1976) compared production values for salt marshes along the Atlantic Coast and found a marked increase in yield with decreasing latitude. If this trend is present on the Pacific Coast, high yields, and perhaps high detrital export, may be expected to characterize southern California coastal marshes.

Salt Marshes of Southern California

Of the 229 km^2 of coastal salt marsh in California, approximately 10 percent occurs in the southern coastal counties of Santa Barbara, Ventura, Los Angeles, and San Diego (Speth 1970). Marshes occur in bays and lagoons (Figure 1) and may generally be considered in two groups--those in continuous contact with the ocean and those with seasonal or occasional contact (Purer 1942, Macdonald 1977). The former are subjected to regular tidal inundation; the latter are closed off by down-coast movement of beach sand except during periods of abnormally high tide or high terrestrial runoff--both of which are most common in the winter. Diked marsh, formerly open to tidal inundation but now removed from tidal influence, comprises a third group.

Southern California coastal marshes have been recognized as important nesting and feeding areas for migratory birds (Frey et al. 1970, U.S. Department on Interior 1972, Speth et al. 1976), and it is likely that energy export, expecially from open marshes, is important to coastal fisheries resources. However, most southern California marshes are threatened by urban development. Indeed, many marshes have been reduced in area or completely destroyed by encroaching urbanism. For example, Los Angeles County once contained 2720 ha of salt marsh located mostly at Ballona Creek. At present, only 32 ha of degraded marsh remain at Ballona Creek as a result of marina construction and creek channelization (Darby 1964, Speth 1970). Mission Bay in San Diego County has suffered a similar loss of marsh; 8.4 ha remain of the nearly 960 ha once found there.

Figure 1. Southern California salt marshes. Asterisk denotes seasonally closed ocean inlet. North is toward top of the figure.

CONCLUSIONS

The following conclusions may be drawn from this investigation.

1. Estimates of net aerial primary production computed as the sum of individual species production with accounting for interval death and shedding and disappearance of dead material are higher than those computed by the traditional approach of Smalley (1959), are better suited to polyspecific stands than those of Smalley (1959) and Wiegert and Evans (1964), and are felt to be close to true net aerial primary production after herbivory.

2. Macrophyte production varies within and between southern California salt marshes.

3. Macrophyte production, especially in Salicornia virginica and Frankenia grandiflora, may be increased by reduced tidal contact.

4. Habitat, especially drainage and salinity, exerts greater control over macrophyte production in the marsh than does tide level alone.

5. Production estimates from this study, together with those of Eilers (1979), support an increase in salt marsh production with decreasing latitude.

6. Production levels in southern California salt marshes are equal to or greater than those of salt marshes at the same latitude on the Atlantic Coast.

7. Future investigations of salt marsh production should be coordinated by a similar method to facilitate comparison of results and recognition of trends.

METHODS

Study Areas

Four study areas were selected to represent the variety and latitudinal extent of coastal salt marshes in southern California.

Sweetwater River Estuary (SRE)

The Sweetwater River drains 570 km^2 of the Peninsular Range of San Diego County. From its headwater area near Stonewall Peak (el. 1747 m) the river flows westward through Loveland and Sweetwater Reservoirs to the eastern edge of San Diego Bay, 10 km north of the Mexican border, between the cities of Chula Vista and National City.

Salt marsh occupies estuarine deltaic deposits at the mouth of the river (Figure 2), and is floristically diverse with a predominance of mixed stands but Spartina foliosa occurs in pure stands along the Sweetwater River channel and locally Frankenia grandiflora, Batis martima and Salicornia virginica form monospecific stands. The present marsh is much reduced from its former extent. Prior to the initiation of dredge spoil deposition on the marsh (the D Street fill) in 1947, 232 ha of salt and brackish marsh were present. By 1977, total marshland had declined to 83 ha and fragmented into three units: Sweetwater marsh (42 ha), Paradise marsh (23 ha), and E Street-Vener Pond marsh (18 ha).

The Paradise marsh, in addition to being partially filled, has been degraded by off-road vehicle use; diking has reduced tidal access in the E Street-Vener Pond marsh. Even though the dredge deposits exacted heavy toll on viable marsh and forced realignment of the main channel of the Sweetwater River, the surviving Sweetwater marsh is otherwise intact. Mudie (1970a) considered it to be the highest quality marsh area remaining within San Diego Bay. For this reason, and because of its estuarine setting with perennial tidal contact, the Sweetwater marsh was selected as a primary study site.

Previous work concerning the Sweetwater marsh is limited primarily to several ecological inventories compiled by or for government agencies (Earth Sciences Associates 1971, Mudie 1970a, Mudie 1970b, Ford et al. 1971, San Diego Unified Port District 1972, Browning and Speth 1973) and to the assessment of environmental impact by proposed flood control of the Sweetwater River (U.S. Army Corps of Engineers 1976). In a classic study of San Diego County marshes, Purer (1942) referred briefly to floristic composition at Sweetwater and included this marsh in a group with marsh at the south end of the Bay and at the mouth of Otay River for the presentation of monthly soil and water

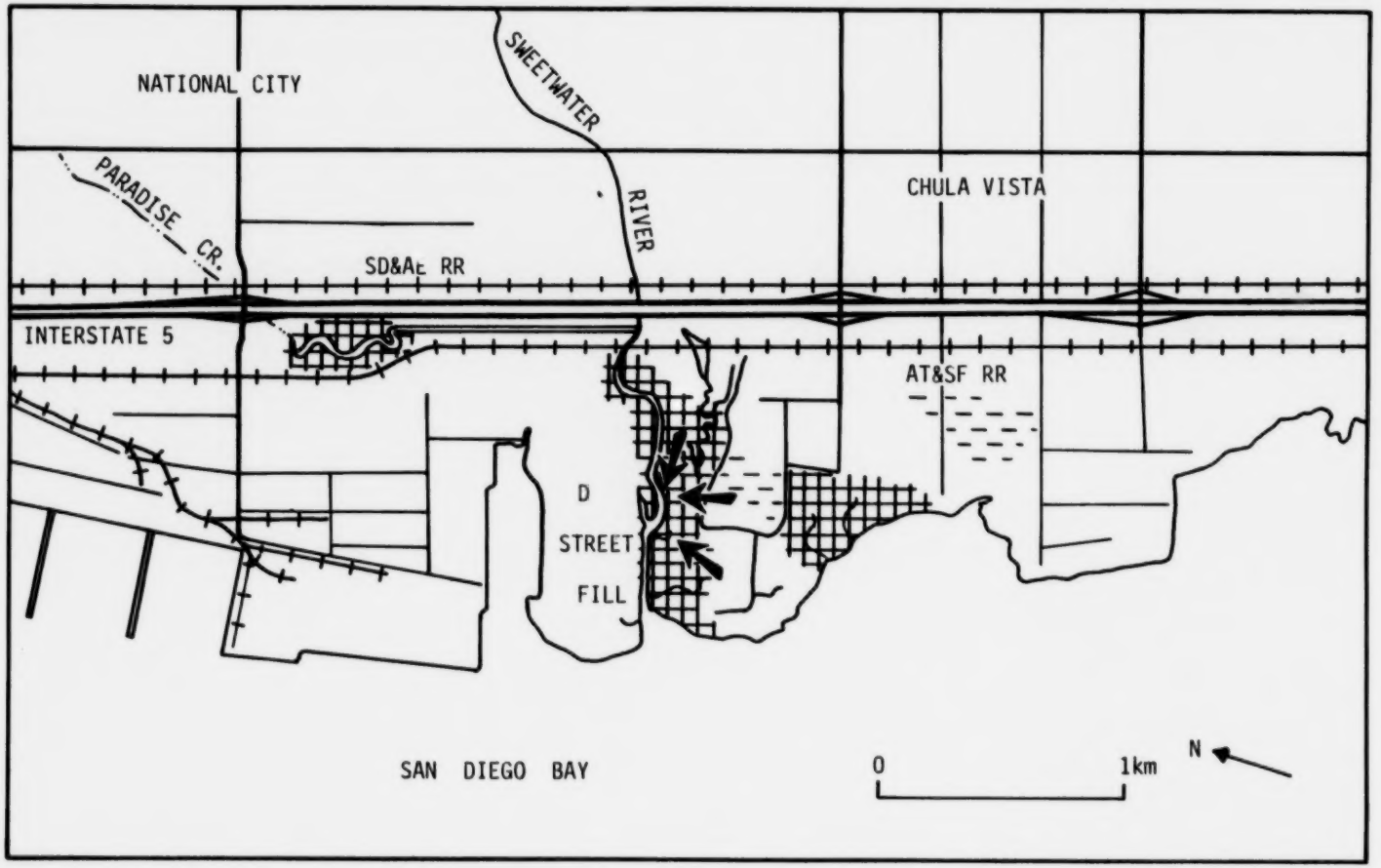

Figure 2. Sweetwater River Estuary. Square pattern denotes salt marsh; dashed lines represent diked and degraded marsh. Paradise marsh at left drains to Sweetwater marsh through a recently excavated channel. E Street-Vener pond marsh is at right center, G Street marsh at right. Arrows from top show position of transects B, A, and C.

salinity measurements. However, Purer (1942) does not specify the Sweetwater Marsh as her sampling site within the group.

Ownership of the Sweetwater marsh is divided between the California Department of Transporation and Santa Fe Land Improvement Co. Vener Farms, Inc. cultivate tomatoes directly to the south. The D Street fill to the north is held by the San Diego Unified Port District.

Los Penasquitos Lagoon (LPL)

Located on the northern city limits of San Diego and 42 km north of Sweetwater, Los Penasquitos Lagoon is the seaward terminus of Soledad and Carmel Valleys (Figure 3). The lagoon name is after a creek in the upper drainage basin, although reference to the wetland as Torrey Pines Lagoon after its proximity to Torrey Pines State Reserve is also seen.

The outstanding characteristics of Los Penasquitos Lagoon are a depauperate flora and limited tidal access. Vigorous Salicornia virginica dominates the marsh in extensive pure stands. Frankenia grandiflora and Distichlis spicata occur locally. Even though the lagoon contains 156 ha of wetland (95 ha of salt marsh) and numerous well-defined tidal channels, some with depth to 9 m, sufficient tidal prism to maintain a perennial breech in the coastal strand is lacking. Only in the winter months when heavy watershed runoff combines with seasonal beach erosion does the tide penetrate the marsh. Summer runoff, when it occurs, may be simply impounded and gradually lost by seepage and evaporation.

Mudie et al. (1974) presented evidence of continuous ocean contact at least until 1888. A combination of railroad and highway construction after this date helped create present conditions by disruption of the drainage system and constriction of the seaward channel. From 1965 to 1970 two sewage treatment facilities discharged secondary overflow into the lagoon. While this added flow helped to maintain more or less permanent ocean access during the period, nutrient enrichment led to the production of thick algae mats and high biological oxygen demand. With the loss of this added flow in 1970, and despite efforts to maintain ocean access (Inman and Nordstrom 1978), contact with the ocean continues to be seasonal.

Los Penasquitos Lagoon was selected as a primary study site because, even with these human modifications, it remains the least altered of lagoons in southern California and is an excellent representative of a wetland with limited tidal control.

Previous study of Los Penasquitos Lagoon includes detailed ecological descriptions (Bradshaw 1968, Bradshaw and Mudie 1972, Mudie et al. 1974) and investigation of physical characteristics (Carpelan 1969). Purer (1942) included Los Penasquitos Lagoon (Soledad Station) among her 12 study sites. Zedler and Mauriello (1979) have made preliminary comparison of salt marsh production at Los Penasquitos Lagoon, Mission Bay and Tijuana River Estuary.

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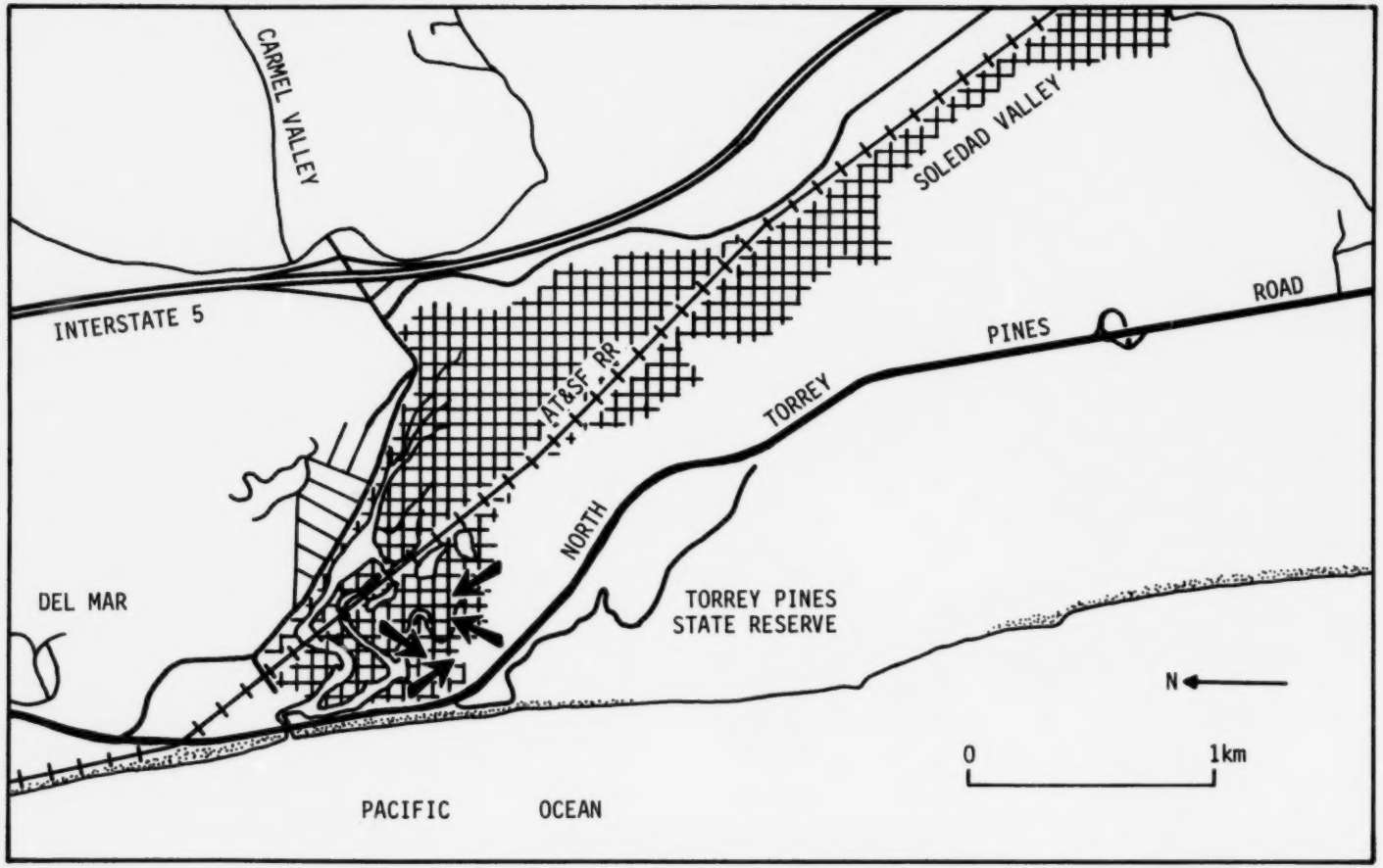

Figure 3. Los Penasquitos Lagoon. Square pattern denotes general extent of salt marsh. Marsh above and to the right of Atcheson, Topeka and Santa Fe tracks is partially degraded with low vegetation density and contains some brackish marsh. Arrows clockwise from top show position of transects D, C, B, and A.

Title to Los Penasquitos Lagoon, including the salt marshes, is held by the State of California. Most of the marsh area is classified as a preserve and is under the jurisdiction of the State Department of Parks and Recreation.

Upper Newport Bay (UNB)

Newport Bay, 110 km north of Los Penasquitos Lagoon, is continuously open to the Pacific Ocean. Two strikingly different subdivisions separated by the Pacific Coast Highway (U.S. 101 Alt.) comprise the bay (Figure 4). Lower Newport Bay is a busy small craft harbor with high density urban development on the surrounding shore. Former salt marsh there has been totally replaced by slips and structures. Upper Newport Bay, by contrast, is little developed, surrounded by cliffs 10 to 30 m high (Newport Mesa), and, while some marsh has been converted to dwellings, about 58 ha still remains. The marsh vegetation is floristically diverse, but generally low in stature. Spartina foliosa is important along creek and pure stands of monanthocloe littoralis occur at highest levels.

Upper Newport Bay is an important avian nesting and feeding area. Seventy species of birds are common to the bay and 89 others are occasional visitors (Frey et al. 1970).

Although the Santa Ana River discharged into Lower Newport Bay for a time around 1900, and may have occupied the upper bay in the geological past (Stevenson 1954), fresh water input to the upper bay is now from three low volume sources--San Diego Creek, Delhi Channel, and Big Canyon Creek. Aside from high nutrient loads, these sources transport great volumes of suspended sediment during the winter from the rapidly urbanizing watershed. High turbidity and rapid siltation of channels is of increasing concern (Stevenson 1978). Dredging of the main channel has been deemed necessary in the past and some spoils have been deposited on salt marsh (primarily near the distal end of Shellmaker Island).

Upper Newport Bay was selected as a primary study site to represent salt marsh in a bay setting with unrestricted tidal fluctuation. Its status as ecological reserve, latitudinal position, and presence of large areas of largely undisturbed salt marsh were also considerations.

Studies of salt marsh plant ecology in Upper Newport Bay are limited to the work of Stevenson (1954), Stevenson and Emery (1958), and Vogl (1966). Descriptive treatment of the upper bay in general is provided by Frey et al. (1970) and Stevenson (1978).

Bolsa Bay (BB)

Bolsa Bay, 16 km north of Newport Bay and about 800 ha in area, occupies the seaward end of an alluvial-filled valley originally excavated at lower sea level in the Bolsa Chica-Huntington Mesa of western Orange County (Figure 5). Two subdivisions comprise the present bay. Outer Bolsa, directly to the west of the Bolsa Chica Mesa, is tidally controlled through a narrow channel

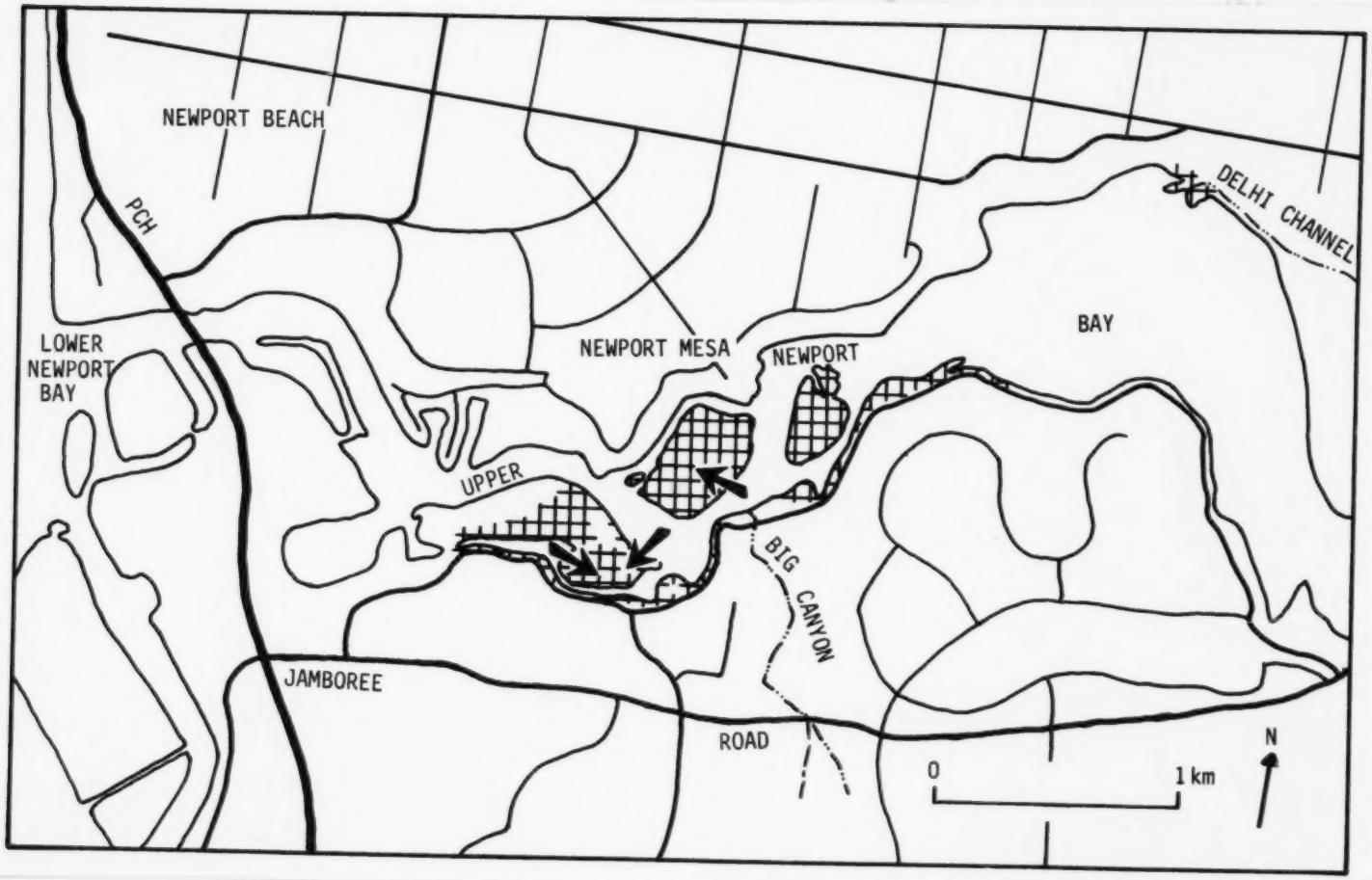

Figure 4. Upper Newport Bay. Square pattern represents salt marsh, and arrows from left show location of transects B and A on Shellmaker Island, and C on Middle Island. PCH is Pacific Coast Highway. Incised area above "Upper" is housing development on former marsh investigated by Stevenson (1954).

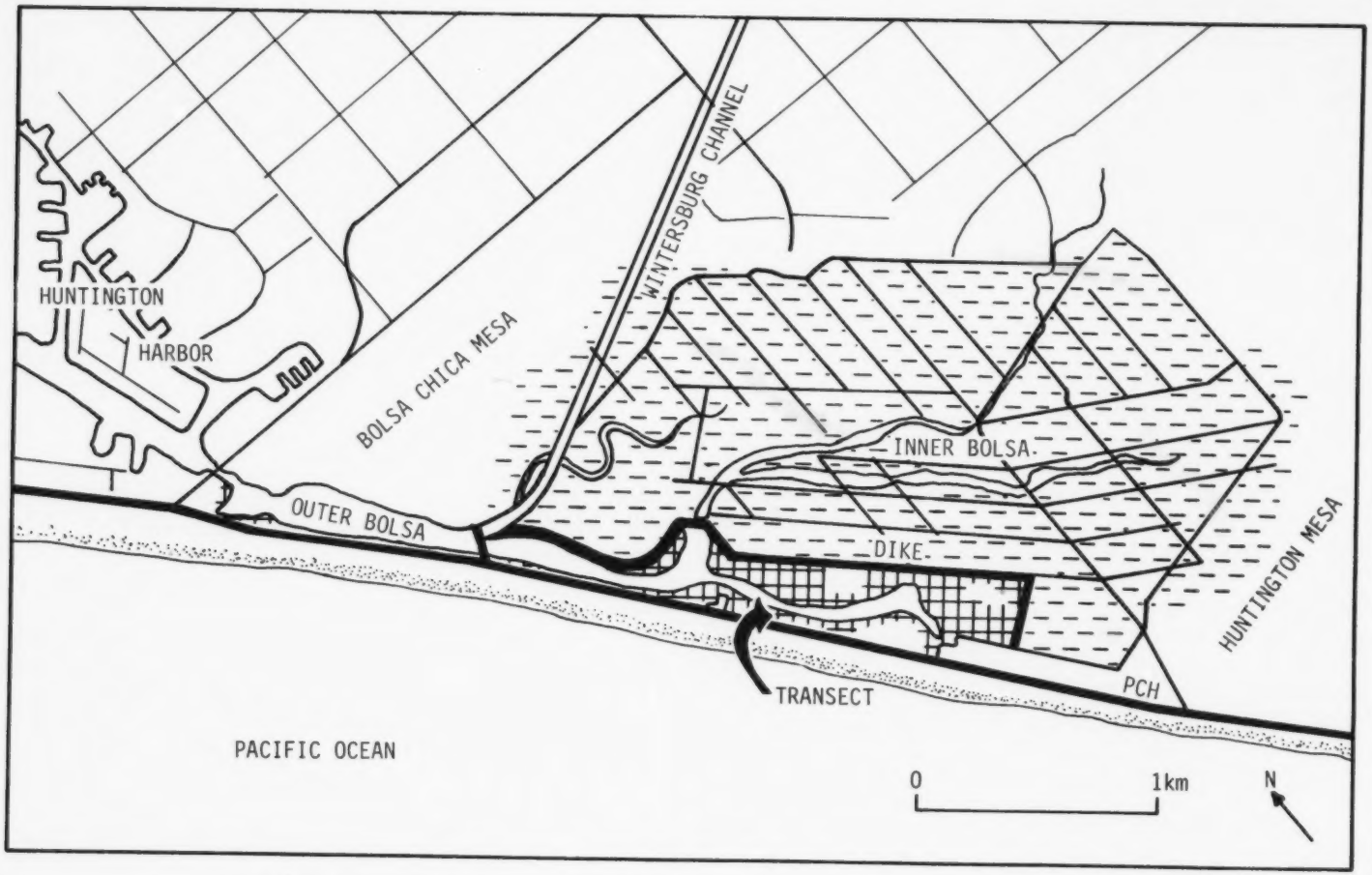

Figure 5. Bolsa Bay. North-south dike separates Inner from Outer Bolsa. Dashed lines denote degraded salt marsh contained largely within land owned by Signal Oil Company. Square pattern is salt marsh within Bolsa Chica Ecological Reserve. PCH is Pacific Coast Highway.

leading to adjacent Sunset Bay. A dike emplaced in 1899 by a private hunting club, and containing culverts with flap valves to prevent incursion of flood tides, extends from the southern edge of the mesa to the beach and separates Outer from Inner Bolsa. Salt marsh in Inner Bolsa is floristically poor. Spartina foliosa grows with low vigor on creek margins and Frankenia grandiflora, Distichlis spicata, and Salicornia virginica occur with greater vigor at higher elevations.

Oil was discovered in Inner Bolsa in 1926. Oil and gas exploitation began in 1943 after extensive diking and well pad construction. The State of California gained title to 140 ha of wetland (all of Outer Bolsa and part of the area outside the drilling area in Inner Bolsa) in 1973 and established the Bolsa Chica Ecological Reserve under the jurisdiction of the Department of Fish and Game. After 1973 plans were made to return tidal fluctuation to State-held lands in Inner Bolsa (after dike construction around this portion of the reserve, limited tidal fluctuation was returned after nearly 89 years to Inner Bolsa in November 1978).

Inner Bolsa was included as a primary study site for several reasons: Study of this marsh before the return of the tides would provide some insight into the ecological effects of long-term tidal removal, follow-up studies could be initiated to assess the impact of tidal restoration, and, most important, Inner Bolsa is representative of highly disturbed salt marshes in southern California (others are La Ballona Creek and Santa Ana River).

Several authors provided description of Bolsa Bay natural resources (Moffat and Nichol 1971, Speth et al. 1976, Henrickson 1976). Macdonald et al., (1971) assessed plant succession since removal of tidal fluctuation. The most detailed treatment of the bay including marsh ecology, however, is that completed by Dillingham Environmental Co. (1971) for Signal Properties, the major landowner. More recently, EDAW (1978) reviewed the work of Dillingham (1971) and considered various development alternatives.

Sampling Procedures--Vegetation

Transect location and sample macroplots

With the aid of aerial photography, a system of transects was located in each study marsh. Each transect was so located as to include as much variety in vegetation pattern and habitat as possible. Semi-permanent wood stakes were driven into the marsh at intervals along transects to serve as recovery points for sampling macroplots. Distance between macroplots was adjusted to maximize representation of pattern and habitat, and, in some cases, avoid creek channels. The position of the 11 transects containing 82 sample macroplots is shown in Figures 2 through 5. Transect length and number of macroplots along transects varied within and between study marshes (Table 1).

Table 1. Transect Length and Number of Sample Macroplots.

Marsh	Transect	Length (m)	No. of Macroplots	Marsh Total
SRE	A	132	14	
	B	56	4	
	C	200	13	31
LPL	A	116	8	
	B	13	3	
	C	123	7	
	D	60	3	21
UNB	A	45	6	
	B	70	7	
	C	266	12	35
BB	A	30	5	5
Total	11	---	--	82

Vegetation sampling and treatment of samples

Sample macroplots were rectangular, 2.0 x 2.5 m, with the center of the short leg adjacent to the wood stake and the long axis perpendicular to the right side of the transect (when looking seaward). Vegetation samples were taken at intervals of six to eight weeks for one year beginning October 1977 (Table 2). All above-ground vascular plant material (living and dead) was harvested from within a 20 x 50 cm wire frame systematically located in the macroplot. Each sample was collected from a different position in the macroplot, and care was taken not to disturb future samples by progressively sampling deeper into the plot and by allowing a buffer of at least 50 cm between harvests.

Table 2. Harvest Date 1977-1978

Session	SRE	LPL	UNB	BB
1	Oct. 14-22	Oct. 22-28	Oct. 29-Nov. 11	Nov. 11
2	Dec. 9-10	Dec. 16-17	Jan. 3-7	Jan. 7
3	Feb. 11	Feb. 17-18	Feb. 24-25	Feb. 25
4	April 14-15	April 21	April 21-22	April 28
5	June 7-8	June 12	June 14	June 15
6	July 17	July 18	July 19	July 19
7	Aug. 23	Aug. 23	Aug. 23	Aug. 23

Plant material constituting each sample was placed in an opaque plastic bag, sealed with a short length of twisted wire, and refrigerated as soon as possible to minimize fermentation (Milner and Hughes 1968). In the laboratory, samples were sorted into green, attached dead, and dead of each species with a separate miscellaneous litter component of unsortable dead material. Each fraction was dried in a gravity convection oven (Thelco model 17) at 85°C to constant weight and then weighed on a balance sensitive to .01 g.

Disappearance of dead material

The rate at which dead material disappears from the marsh was estimated by using a variation of the standard litter bag technique (Wiegert and Evans 1964). At the time of the first harvest, a number of macroplots in each study marsh was selected to represent overall diversity of sites, and a mix of plant material approximating the species composition from each selected plot was divided into four plastic screen bags of 1 mm mesh. Litter bags were secured along the edges with staples and cloth tape after the contents of each had been weighed and an aluminum identification tag placed within. A sub-sample of plant material from each set was retained to establish proportionate dry weight at the initiation of the experiment. The bags, containing 50 to 200 g of plant material and measuring 12 x 24 cm, were placed on bare soil in the respective macroplots and kept in place by stout monofilament line fastened to pegs driven into the soil.

At intervals of approximately three months, one bag from each original group of four was removed and its contents, freed from soil and new growth, dried to constant weight. If it appeared that inorganic accumulations were present (as was common for bags from macroplots near mudflats) the contents were combusted in a muffle furnace, and the ash-free dry weight was substituted for the dry weight obtained above.

Disappearance rate of dead material was calculated as

$$r = [(dwt_o - dwt_i) \div dwt_o] \div (t_i - t_o)$$

where r = disappearance rate in g·g·day, dwt_o is dry weight at time zero, dwt_i is dry weight at the end of the interval, and $(t_i - t_o)$ is the interval in days.

Calculation of above-ground net primary production

Estimates of net aerial primary production (NAPP) were computed by three methods. Initially, the procedure of Smalley (1959) was followed whereby net production for intervals between harvests was computed with reference to changes in live and dead biomass, then interval net production was summed over the annual cycle (ST).

Because this application of the Smalley (1959) method does not account for variations in biomass of individual species which may be out of phase with total site biomass (Eilers 1975), a second estimate of annual production was computed (SST). In this case changes in individual species living and dead

biomass were used with the Smalley (1959) approach to yield species annual production. Annual production for component species was then summed and adjusted for changes in miscellaneous litter (positive changes in miscellaneous litter were added according to changes in total live biomass after Smalley 1959).

The final approach (SSTC) to NAPP was a combination of the method of Smalley (1959) and Wiegert and Evans (1964). Here the summation of individual species net annual production (with accounting for miscellaneous litter) was computed as above (SST), then the average disappearance rate for the marsh in question was applied to interval changes in individual species and miscellaneous dead biomass and appropriate losses added.

Sampling Procedures--Substrate

At the time of each vegetation sample harvest, a suite of substrate measurements was taken from each macroplot.

Salinity

Three aspects of substrate salinity were determined after a core sample 50 cm deep and 4 cm in diameter was extracted with a suction device. The upper and lower 5 cm sections were cut from the core, and sub-samples of each were individually wrapped in filter paper (Whatman No. 1), placed in a separate plastic syringe, and squeezed to force out drops of interstitial soil water for which salt content was determined with a Goldberg refractometer (Behrens 1965). As soil free-water percolated into the hole from which the core had been removed, samples were withdrawn by pipette and tested for salinity with the same instrument.

Reaction, redox, ammonia

Soil free-water, as obtained above, was further subdivided and subjected to three additional tests using a specific ion meter (Orion model 407a). Reaction (pH) was determined directly with a combination electrode. Oxidation-reduction potential (Redox) was measured directly with a combination platinum electrode and converted to Eh (Orion 1978). Analysis for NH_3-N by an ammonia electrode followed the adjustment of sample pH to 11 by addition of sodium hydroxide (Banwart et al. 1972).

Water content

After sub-samples of the upper and lower 5 cm of the extracted soil core were taken for measurement of interstitial salinity, the remainder of each was sealed in a plastic bag. In the laboratory, after initial weighing, samples were oven dried to constant weight, re-weighed, and percent water content (c) computed as, $c = [(w-d) \div w] \cdot 100$, where w is sample weight wet and d is sample weight dry.

Temperature

Substrate temperature was measured at 5 cm and 50 cm depths with a long-stem dial head thermometer (Reotemp) placed near harvested quadrats.

Elevation

Elevation at each of 82 macroplots was determined with transit and stadia (Pugh 1975). At Sweetwater and Bolsa, levels were double run to nearby tidal bench marks (National City, R 57 1926 and Los Patos, 3; respectively).

No tidal bench marks were found near Los Penasquitos, but numerous positions in the marsh had been surveyed to National Geodetic Vertical Datum (NGVD) and monumented by the U.S. Army Corps of Engineers. Levels at Los Penasquitos were double run to several of these monuments and then converted to tide level by applying a conversion factor midway between those published by the National Ocean Survey (NOS) for Scripps Institution, La Jolla, and Newport Bay Entrance (Corona Del Mar).

Leveling at Newport was facilitated by recent work of the NOS for the Environmental Protection Agency (NOAA 1978). Here tide level monuments left by this survey served in the double run procedure. Maximum acceptable closing error for all leveling was set at 3 cm.

Tidal Inundation

In-marsh tide level recordings were obtained for periods of six and four weeks at Sweetwater and Newport, respectively, with a recording gauge (Leupold Stevens Model 031). Inundation periods for increments of elevation were to be computed for the two marshes, but because the required simultaneous and long term recordings for nearby primary gauges could not be obtained from the NOS, this aspect of the study cannot be reported.

Water levels at Los Penasquitos were recorded at each sampling period from a stake driven into the mud of a marsh creek, but continuous recordings there were not included in this study. After the return of tidal fluctuation to Inner Bolsa Bay in 1978, tide levels there were monitored with a staff gauge over one 48-hour period.

Habitat Types

In order to test the importance of location within marshes to NAPP, all macroplots were placed in one of seven topographically determined habitat types: 1) Fore Levee Slope, 2) Levee Crest, 3) Back Levee Slope, 4) Back Levee Depression, 5) Slope Below Upland, 6) Upland Transition, and 7) Pan.

Data Analysis

Data analysis followed Snedecor and Cochran (1967). Descriptive statistics were produced for all vegetation and environmental data, analysis of variance provided a means to explore variation of NAPP within and between study areas, and relations between variables were investigated through correlation and multiple regression analyses.

RESULTS

Vegetation

Plant species

Fifteen vascular plant species were recorded in sample quadrats (Table 3). Salicornia virginica was most frequent followed by Frankenia grandiflora and Batis maritima. Rare species included Cressa truxillensis found only at Los Penasquitos, and Lotus scoparius and Cordylanthus martimus found only at Newport. Species diversity (variety) was greatest for Newport nearly as great for Sweetwater, but low for both Los Penasquitos and Bolsa. Monospecific stands comprised 28 percent of the macroplot samples (Table 4), and the mean number of species for the 82 macroplots was 4.4.

Biomass

Macroplot living and dead standing crop biomass for harvest sessions is found in Appendix A. Macroplot LPL-15 recorded the living biomass high of 3915 g m^{-2} (session 1) but, while two macroplots located near creek channels (LPL-13, BB-5) showed no living material for two or more sessions, all others had living material all year. With the exception of UNB-17 and SRE-26, all macroplots contained dead biomass throughout the year. Maximum dead biomass for all sites was 4749 g m^{-2} (SRE-8, session 6), and the annual mean for living and dead material over all macroplots was 751 and 797 g m^{-2}, respectively.

Twenty-eight percent of the macroplots recorded a single living biomass peak, but most macroplots recorded two peaks (72%). Single peaks occurred most often in the summer, while dual peaks were most common winter-summer and summer-fall. No clear relationship between the number of different species, site elevation and the presence of single or dual peaks was detected, but the common occurrence of dual peaks suggested that the vegetation responds to summer warmth and fall, winter, and spring precipitation.

For dead biomass in macroplots dual peaks were likewise most common (78% of macroplots) with winter-summer most frequent. Dual peaks in dead biomass tended to occur concomitant with dual peaks in live biomass.

Mean living and dead biomass (Figure 6) reflected the persistence of dual peaks in dead biomass but tended to mask dual living biomass peaks. Mean living biomass minima occurred in March samples and greatest mean living biomass was found in June samples for all marshes with the exception of Los Penasquitos were the maximum was present in November 1977 (an August peak was

Table 3. Species Frequency in Quadrat Samples.

Species	Species Abbr.	Marsh				Total Freq(82)
		SRE(31)[a]	LPL(21)	UNB(25)	BB(5)	
Batis maritima L.[b]	Bama	23		19		42
Cressa truxillensis HBK. var. vallicola (Heller) Munz	Crtr		1			1
Cuscuta salinia Engelm.	Cusa	4	2	2		8
Distichlis spicata (L.) Greene var. spicata	Disp	11	1	13	3	28
Frankenia grandiflora Cham. & Schlect.	Frgr	21	6	13	2	42
Jaumea carnosa (Less.) Gray	Jaca	11		13		24
Limonium californicum (Boiss.) Heller	Lica	16		11		27
Lotus scoparius (Nutt.) Ottley spp. scoparius	Losc			1		1
Monanthocloe littoralis Englem.	Moli	8		6		14
Cordylanthus maritimus Nutt.	Orpu			1		1
Salicornia bigelovii Torr.	Sabi	14		10		24
Salicornia virginica L.	Savi	28	20	19	3	70
Spartina foliosa Trin.	Spfo	9		16	3	28
Suaeda californica Wats.	Suca	16		4		20
Triglochin maritimum L.	Trma	17		13		30
Number of Species		12	5	14	4	15

[a] Total number of sample macroplots
[b] Nomenclature after Munz (1974)

Table 4. Species Diversity of Macroplot samples.

No. of Species	No. of Macroplots	%	No. of Species	No. of Macroplots	%
1	23	28	6	6	7
2	10	12	7	11	14
3	4	5	8	5	6
4	6	7	9	6	7
5	7	9	10	3	4

apparent in 1978). Relatively large standard errors for living and dead biomass means, especially for Los Penasquitos and Bolsa, emphasized the heterogeneity of vegetation along transects.

Disappearance of dead material

Dead plant material in most litter bag sets decomposed rapidly in the first interval after placement in the marsh, then the rate of disappearance declined (Table 5). This was expected because bags contained some recently living plant parts, and leaching of organic matter is most rapid in the first few days after death occurs (Odum et al. 1972). Site mean rates ranged from .67 to 3.74 mg g^{-1} day^{-1}; a single bag recovered from BB-4 after 106 days recorded the highest rate (9.43 mg $g^{-1}day^{-1}$), and the grand mean for LPL was well below that for the other study marshes. The lower rate at LPL was probably related to the woody Salicornia virginica placed in bags and dryness resulting from infrequent tidal submergence.

Net Production of Stands

NAPP varied with the method of computation (Tables 6 and 7). The Smalley (1959) method applied to changes in living and dead biomass without accounting for growth in individual species (ST) provided estimates that were an average of 1.44 times less than Smalley method applied to component species (SST) and 1.46 times less than SST corrected for decomposition of dead material between sample intervals (SSTC). Thus the Smalley method as orignally applied (Smalley 1959) appears to have severely underestimated NAPP, especially for multispecies stands, and much better estimates were provided for all stands when species growth patterns and litter decomposition were included. Yet, while SSTC was considered the best estimate of the three computed for each macroplot, values could be improved by accounting for losses to herbivory.

Production estimates (SSTC) ranged from 164 g $m^{-2}yr^{-1}$ at BB-5 to 6369 g $m^{-2}yr^{-1}$ at LPL-9 with an overall mean for the four study marshes of 2986 g $m^{-2}yr^{-1}$. Los Penasquitos Lagoon was clearly the most productive marsh; Upper Newport Bay the least. Analysis of variance between marsh means showed that differences in production were significant ($P<.001$).

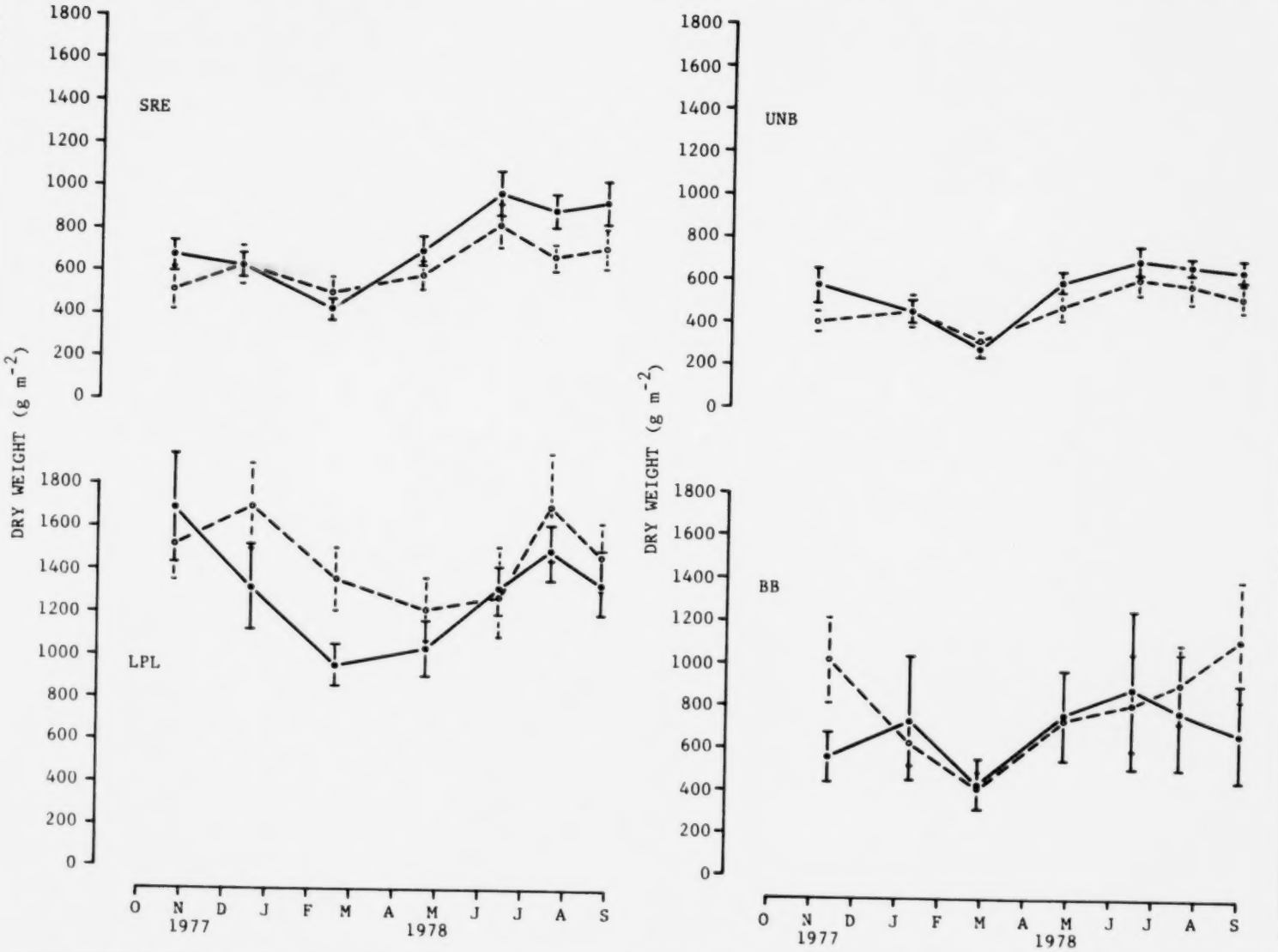

Figure 6. Living and dead standing crop biomass means ± S.E. (g m^{-2}) through the sample period for study areas. Solid line denotes living biomass, dashed line is dead biomass.

Table 5. Disappearance Rates for Dead Material Computed from Dry Weight of Litter Bag contents. Litter Bag Sets Placed as Follows: SRE, 10/22/77; LPL, 10/28/77; UNB, 11/11/77; BB, 11/11/77.

Marsh		Days in Marsh	Rate mg·g·day	Site $\bar{x}$ mg·g·day
SRE	1	113	3.45	
		306	.98	
		357	1.23	1.89
	9	113	5.92	
		229	1.97	
		306	1.90	
		357	1.62	2.85
	13	113	5.66	
		229	2.71	
		306	2.25	
		357	2.10	3.18
	14	113	1.59[a]	
		229	4.06[a]	
		306	2.94[a]	
		357	2.27[a]	2.27
	15	113	.71	
		229	.26	
		357	1.04	.67
	16	113	4.51	
		229	1.83	
		306	1.76	
		357	2.21[a]	2.57
			Grand $\bar{x}$	2.38
LPL	4	113	2.57	
		301	.36	
		351	.26[a]	1.06
	13	113	2.83	
		228	1.62	
		301	1.83	
		351	2.02	2.08
	15	228	2.37	
		301	2.17[a]	
		351	1.47[a]	2.00
	20	113	1.50	
		228	3.08[a]	
		301	1.58[a]	
		351	1.89[a]	2.18
			Grand $\bar{x}$	1.83
UNB	1	106	2.26	
		215	1.40	
		288	1.15	
		337	1.07	1.47
	3	106	6.42	
		215	3.07	
		288	2.67	
		337	2.79	3.74
	7	106	4.31[a]	
		2.5	2.27[a]	
		288	2.26[a]	
		337	2.14	2.75
			Grand $\bar{x}$	2.65
BB	2	106	4.43	
		145	3.50[a]	
		216	1.06	
		292	1.58	2.64
	4	106	9.43[a]	9.43
			Grand $\bar{x}$	2.64[b]
				(9.43)

[a] Computed from ash free dry weight
[b] Two values were used at BB.

Table 6. Annual Net Production Estimates (g $m^{-2}yr^{-1}$) Based on Three Methods of Computation. ST is Method of Smalley (1959); SST is Sum of Individual Species Production based on Smalley (1959); SSTC is SST Corrected for Disappearance of Dead Material.

Marsh	ST	SST	SSTC	Marsh	ST	SST	SSTC
SRE 1	3256	3284	3576	LPL 6	4990	5438	5710
2	993	1703	1769	7	2131	2131	2289
3	3517	5708	5824	8	3006	4396	4616
4	2361	3163	3321	9	2784	5778	6369
5	1918	3019	3135	10	2909	2909	3056
6	2447	3554	3723	11	5073	5073	5303
7	3484	4100	4220	12	2390	4615	5416
8	3800	5459	5573	13	1464	1464	1767
9	2280	3133	3243	14	2531	2531	2690
10	1410	2143	2232	15	5649	5649	5848
11	1750	2857	3048	16	2896	2896	3224
12	1633	2346	2412	17	1737	1737	2047
13	1869	3692	3789	18	4968	4968	5219
14	1614	1614	1824	19	2563	4431	4737
15	620	620	665	20	2264	2264	2417
16	491	1414	1430	21	1501	1501	1582
17	3691	5184	5402				
18	2457	2457	2659	$\bar{x}$	3084	3539	3787
19	5734	5734	6231	S.D.	1259	1448	1528
20	1318	3100	3192				
21	1047	3016	3096				
22	1376	4674	4768	UNB 1	1356	1556	1708
23	1531	2643	2718	2	1265	1648	1790
24	1702	3264	3355	3	1609	2461	2574
25	2355	3388	3429	4	1287	2154	2234
26	885	1770	1782	5	1040	2057	2292
27	1364	2993	3102	6	1215	1215	1339
28	1848	2979	3208	7	1187	1572	1687
29	1284	1289	1318	8	2540	4007	4104
30	2121	2479	2532	9	918	1819	1849
31	1349	2469	2492	10	1646	2390	2552
				11	1331	1931	1847
$\bar{x}$	2049	2943	3196	12	1371	2142	2263
S.D.	1117	1203	1330	13	2389	2389	2621
				14	1214	2607	2691
LPL 1	4777	4777	5011	16	780	1125	1161
2	1924	1924	2088	17	1005	1354	1380
3	3137	3137	3155	18	1322	2289	2331
4	2972	2972	3067	19	592	954	976
5	3113	3736	3922	20	1168	1224	1376

continued

Table 6. (cont.)

Marsh		ST	SST	SSTC
UNB	21	1133	2321	2414
	22	895	1380	1393
	23	2906	2906	3217
	24	3432	3933	4055
	25	1722	1722	1969
	$\bar{x}$	1469	2035	2150
	S.D.	673	770	795
BB	1	4282	4380	4638
	2	1152	2214	2372
	3	2058	3522	3622
	4	1158	1561	1676
	5	164	164	164
	$\bar{x}$	1762	2368	2494
	S.D.	1559	1652	1731
ALL	$\bar{x}$	2120	2833	2986
	S.D.	1220	1339	1408

Table 7. Ratios of Production Estimates Derived by the Smalley Method (ST) to Sum of Individual Species (SST) and Sum of Individual Species Corrected for Interval Decomposition (SSTC).

	ST	SST	SSTC
SRE	1.00	1.65	1.71
LPL	1.00	1.17	1.26
UNB	1.00	1.45	1.53
BB	1.00	1.49	1.35
ALL	1.00	1.44	1.46

Net Production of Species

Species net production estimates based on the Smalley (1959) method corrected for interval decomposition (SSTC) are presented by macroplot in Appendix B and summarized by marsh in Table 8. It may be found that summing of component species production in macroplots yields a value less than total SSTC for the site as presented above. The reason for this discrepency is that harvested dead standing crop biomass often graded from parts recognizable as to species to amorphous duff with no recognizable species affinity. Accounting for this miscellaneous plant material, therefore, could not be included in species estimates (this material was included in macroplot estimates).

Overall, the most productive plant species were Frankenia grandiflora, Salicornia virginica and Spartina foliosa. On an individual marsh basis, these species were most important at Sweetwater but at Newport Frankenia was conspicuously subdued, especially on transects A and B where it was all but replaced by Monanthocloe littoralis. Spartina was not present at Los

Table 8. Summary of Net Production for Plant Species (g $m^{-2}yr^{-1}$).

Marsh	Species	$\bar{x}$	Min.	Max.	Freq.	Marsh	Species	$\bar{x}$	Min.	Max.	Freq.
SRE	Bama[a]	264	6	980	23	UNB	Savi	634	10	3160	19
	Cusa	72	2	238	4		Spfo	819	9	3217	16
(31 sites)	Disp	240	4	1426	11		Suca	120	10	142	4
	Frgr	880	4	6231	21		Trma	204	20	511	13
	Juca	442	1	2395	11						
	Lica	200	1	862	16	BB	Disp	901	74	1452	3
	Moli	232	43	562	8		Frgr	2318	72	4564	2
	Sabi	231	1	713	14	(5 sites)	Savi	1035	459	1525	3
	Savi	1176	22	3732	28		Spfo	486	164	1032	3
	Spfo	611	3	2659	9						
	Suca	161	1	882	16						
	Trma	159	7	792	17						
LPL	Crtr	127			2	All	Bama	221	5	980	42
	Cusa	1			1	MARSHES	Coma	8			1
(21 sites)	Disp	1184			1	TOGETHER	Crtr	127			2
	Frgr	3274	1871	4864	6		Cusa	42	1	238	7
	Savi	2789	1176	5848	20	(82 sites)	Disp	362	4	1561	28
							Frgr	1046	4	6231	42
							Juca	338	1	2395	24
UNB	Bama	168	5	620	19		Lica	203	1	862	27
	Coma	8			10		Losc	5			1
	Cusa	3	1	5	2		Moli	509	6	1351	14
(25) sites)	Disp	278	8	1561	13		Coma	8			1
	Frgr	90	4	491	13		Sabi	173	1	713	24
	Jaca	249	21	554	13		Savi	1483	10	5848	70
	Lica	209	3	816	11		Spfo	716	3	3217	28
	Losc	5			1		Suca	153	1	882	20
	Moli	877	6	1351	6		Trma	178	7	792	30
	Sabi	93	1	466	10						

[a] Species abbreviations from Table 3.

Penasquitoes. Distichlis spicata was more productive than Spartina at Bolsa. Indeed, Spartina at Bolsa appeared to partially die back in early 1978 with only poor aerial growth evident the following summer, expecially at BB-5. Low production species--Cuscuta salina, Lotus scoparius, Cordylanthus maritimus--were of limited occurrence.

Substrate

Salinity

Substrate interstitial salinity at the upper root zone (0 to 5 cm) and sub-root zone depth (45 to 50 cm) by harvest session is found in Appendices C.1 and C.2. Appendix C.3 contains salinity values for substrate free water. The peak root zone salinity recorded was 125 ppt (LPL-17, session 2); the minimum root zone value was 5 ppt (UNB-7, session 2; UNB-7 and UNB-8, session 3). The sub-root zone salinity maximum of 105 ppt occurred at SRE-15 (session 7); the minimum of 3 ppt occurred at UNB-1 (session 3). Free-water salinity minimum and maximum were, respectively, 103 ppt (SRE-15, session 3) and 3 ppt (UNB-1, session 2 and 3). In general, root zone salinity for most macroplots was low in spring (sessions 3 and 4) and high in summer (sessions 5, 6, 7). Sub-root zone salinity followed somewhat similar patterns, and free water salinity tended to be intermediate between root and sub-root zones.

Comparison of mean harvest session salinities by depth and marsh (Figure 7) showed a summer peak for Sweetwater, Newport and Bolsa, a winter peak for Los Penasquitos. Comparison of salinities over the year in the root zone and sub-root zone revealed that winter precipitation reduced surface concentration and increased salinity at depth, while summer drought tended toward greater concentration of salts at the surface. Los Penasquitos and, to a degree Bolsa, were somewhat out of phase with Sweetwater and Newport with higher surface salinities persisting through fall and winter and lower suface salinities in the summer. Perhaps the lack of tidal inundation during the summer at Los Penasquitos and Bolsa was responsible, but the reason for this is obscure. Annual mean salinities for the two depths were remarkably close, suggesting that overall variation for the substrate profile was slight. Overall "saltiness" as revealed by annual means was greatest at Sweetwater, least at Bolsa, and intermediate at Newport and Los Penasquitos, although the former recorded greater mean surface salinity than the latter.

Reaction

Substrate pH (Appendix C.4) ranged from 5.2 (UNB-17, session 7) to 8.8 (UNB-1, session 2). Marsh harvest session means (Figure 8) for Sweetwater, and Newport peaked in the neutral range in the spring and revealed a shift to slightly acid conditions in the summer; means for Los Penasquitos peaked at slightly basic in the fall and reached a minimum of slightly acid in the early summer; means for Bolsa remained neutral to slightly basic throughout the year.

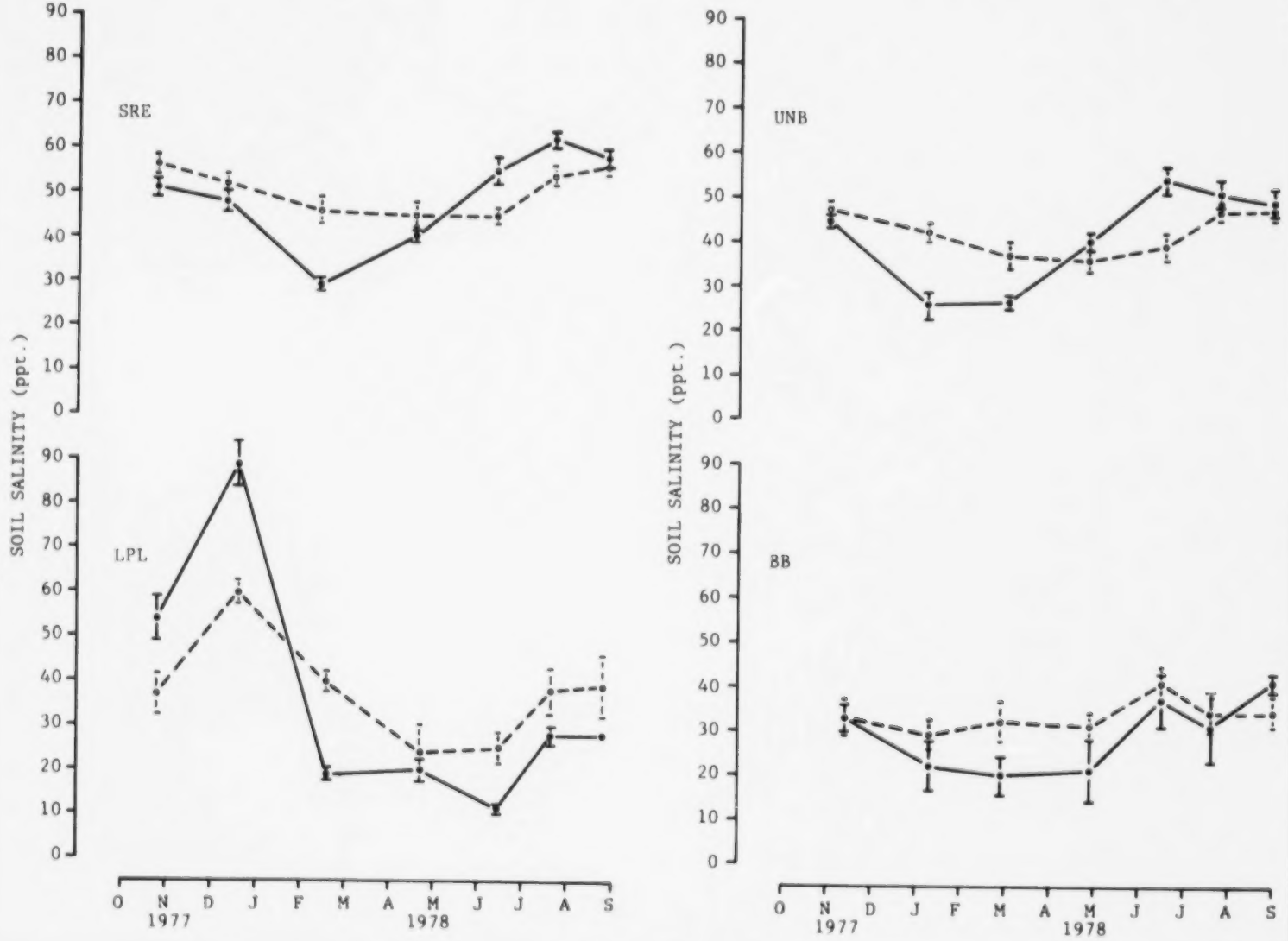

Figure 7. Mean interstitial salinity (ppt) of substrate at 0-5 cm depth (solid line) and 45-50 cm (dashed line) ± S.E. for study areas through the sample period.

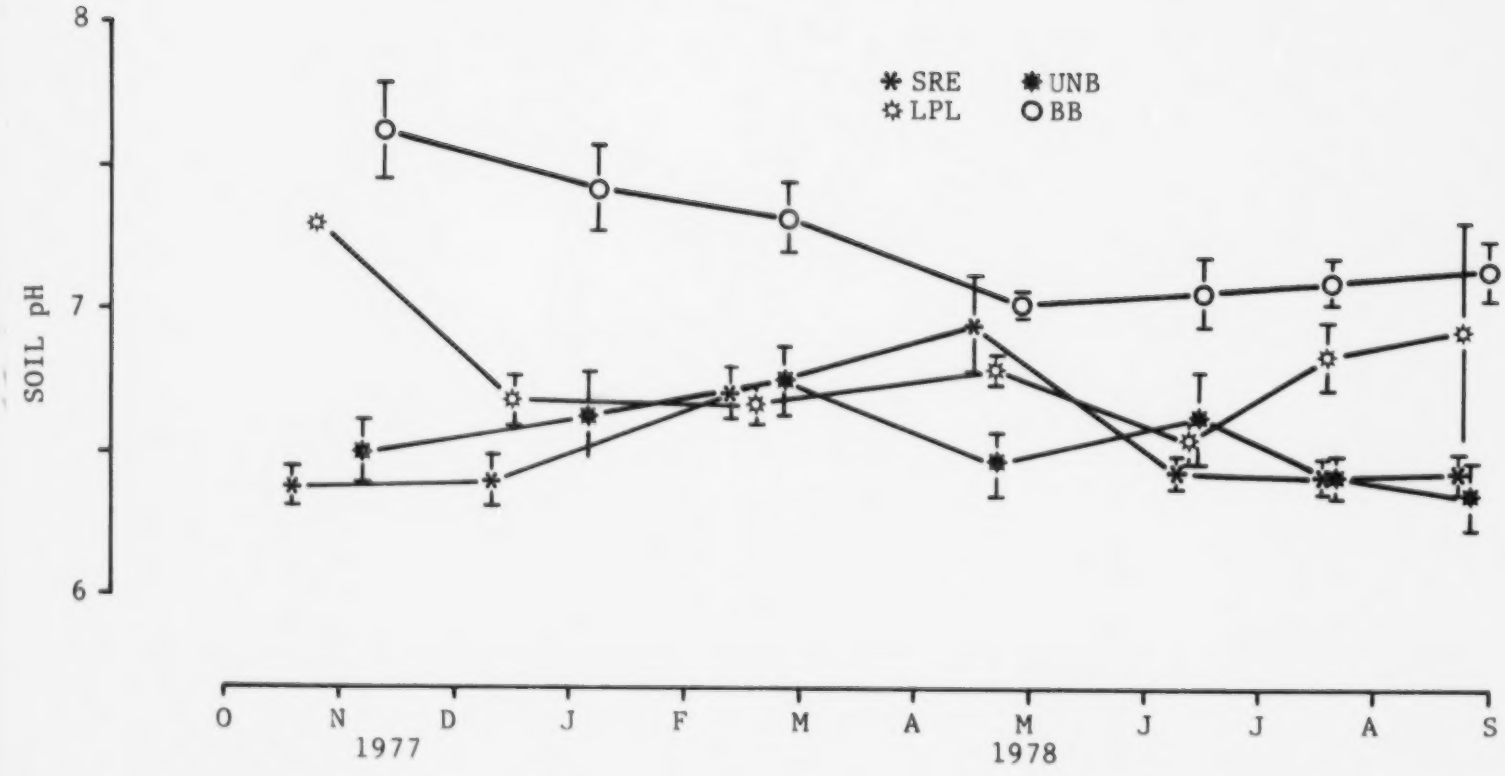

Figure 8. Mean pH of substrate soil free-water ± S.E. for study areas through the sample period.

Ammonia

Ammonia in substrate free-water varied greatly (Appendix C.5). The lowest value of 1 x 10^{-5}M occurred in numerous macroplots in spring; the high value was 120 x 10^{-5} M (UNB-25, session 1). Occasionally an insufficient quantity of soil free-water to test with the specific ion electrode was recovered, but it was felt that the data available did adequately represent trends in NH_3. Mean NH_3 values were generally highest in summer and lowest in spring (Figure 9). Sweetwater and Newport showed an increase in soil ammonia from spring to early summer, then a decrease in middle and late summer followed by a second increase in fall. Ammonia at Bolsa did not follow this dual maxima pattern, and the lack of data for session 1 at Los Penasquitos leaves a question of where this marsh fits. With reference to annual means, Bolsa was clearly the best supplied with NH_3, followed by Newport.

Redox

Redox potential (Eh) of substrate free-water (Appendix C.6) was lowest at BB-4 (-126 mV, session 3) and highest at UNB-12 (542 mV, session 2). Low (<200 mV) and negative potentials were most persistent at Bolsa; Sweetwater displayed most consistantly high potentials. Gaps in the redox record (e.g., LPL, session 1; SRE, Session 2) were caused by a malfunction of the platinum electrode and, after the defective electrode was replaced, by insufficient soil free water to obtain a measurement. Even though data for all macroplots over all sessions was lacking, mean redox values (Figure 10) did reveal that low potentials, and hence prolonged anaerobic conditions--values <200 mV suggest the presence of reduced iron and manganese (Hesse 1972, Stolzy and Flühler 1978)--were characteristic only of Bolsa and that the other study marsh substrates were predominately aerobic. This was not surprising, through, because only at Bolsa were sample sites waterlogged at each visit, and only there was H_2S frequently sensible.

Water content

Appendices C.7 and C.8 present root zone and sub-root zone percent water content of substrate samples. Minimum and maximum for each depth were 0 (UNB-7, session 5) and 89 (BB-3, session 3; BB-5, session 4), and 16 (LPL-8, session 1) and 70 (UNB-5, session 4), respectively. Means for harvest sessions (Figure 11) revealed that root zone water content was very frequently above water content at depth. This is explained by the nearly universal nature of substrate profiles--superficial fine-grained silts and clays, often with high organic content, over sand and silty sand with low organic content. Thus, even when both depths were saturated, the root zone carried the greater water proportion. A curious variation on this theme was discovered on transects UNB-A and UNB-B. Here the upper ends of both transects extended onto old dredge spoil deposits of high sand and shell content. Because spoil overlayed the old marsh surface, water content was often greater in deeper samples. However, lower extensions of both transects support the more common pattern.

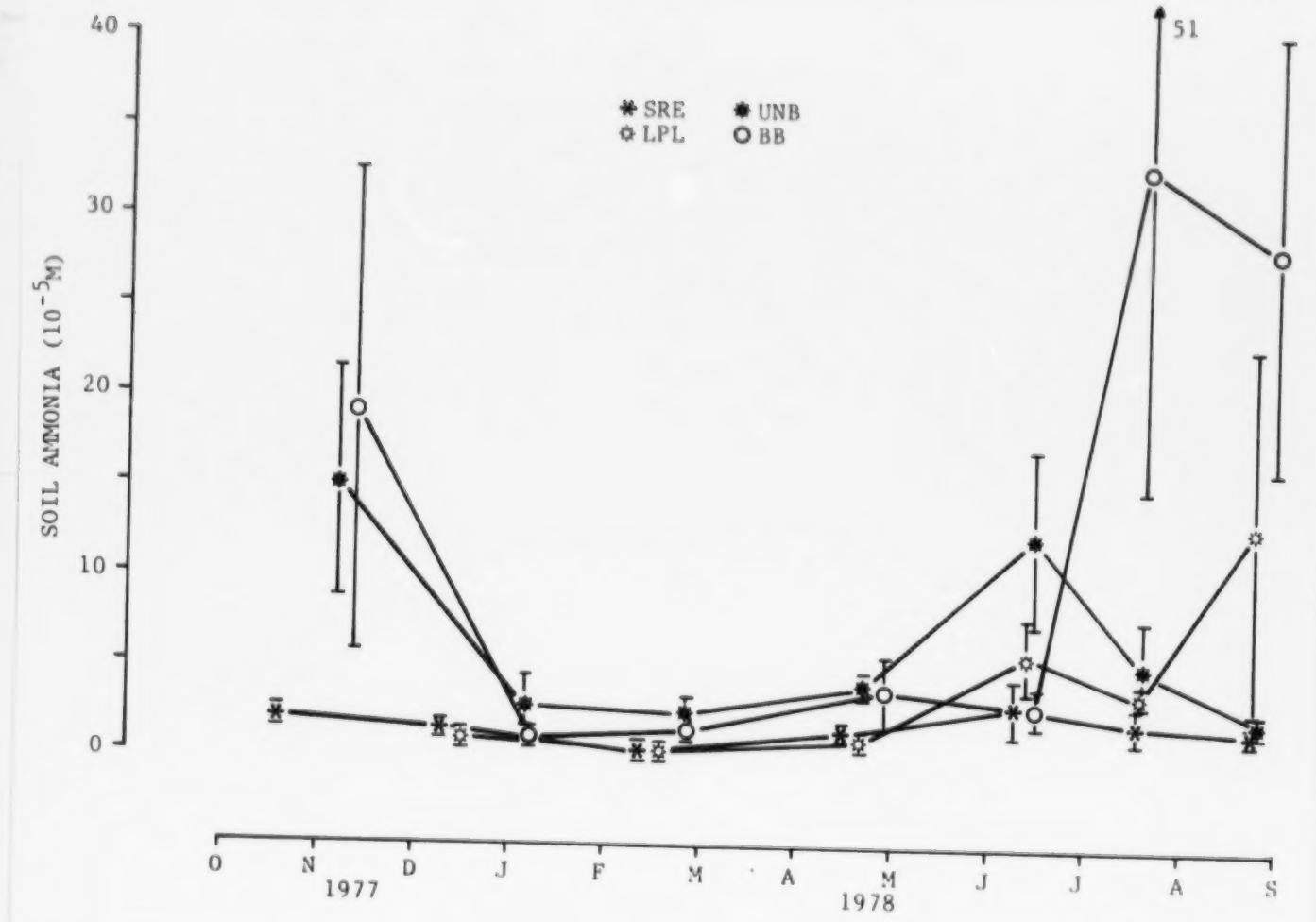

Figure 9. Mean ammonia (10^{-5}m) of substrate free-water ± S.E. for study areas through the sample period.

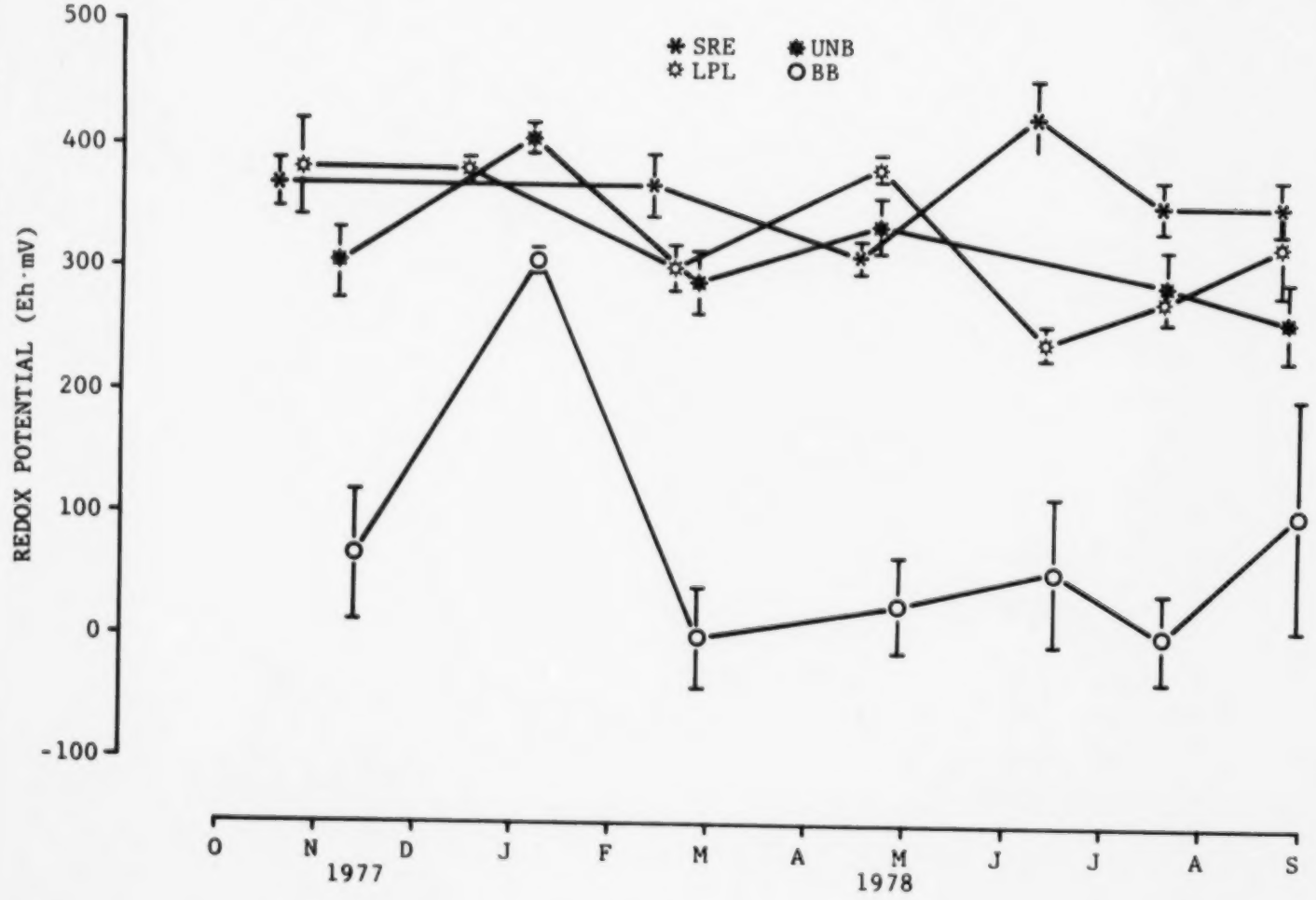

Figure 10. Mean redox potential (Eh·mV) of substrate free-water ± S.E. for study areas through the sample period.

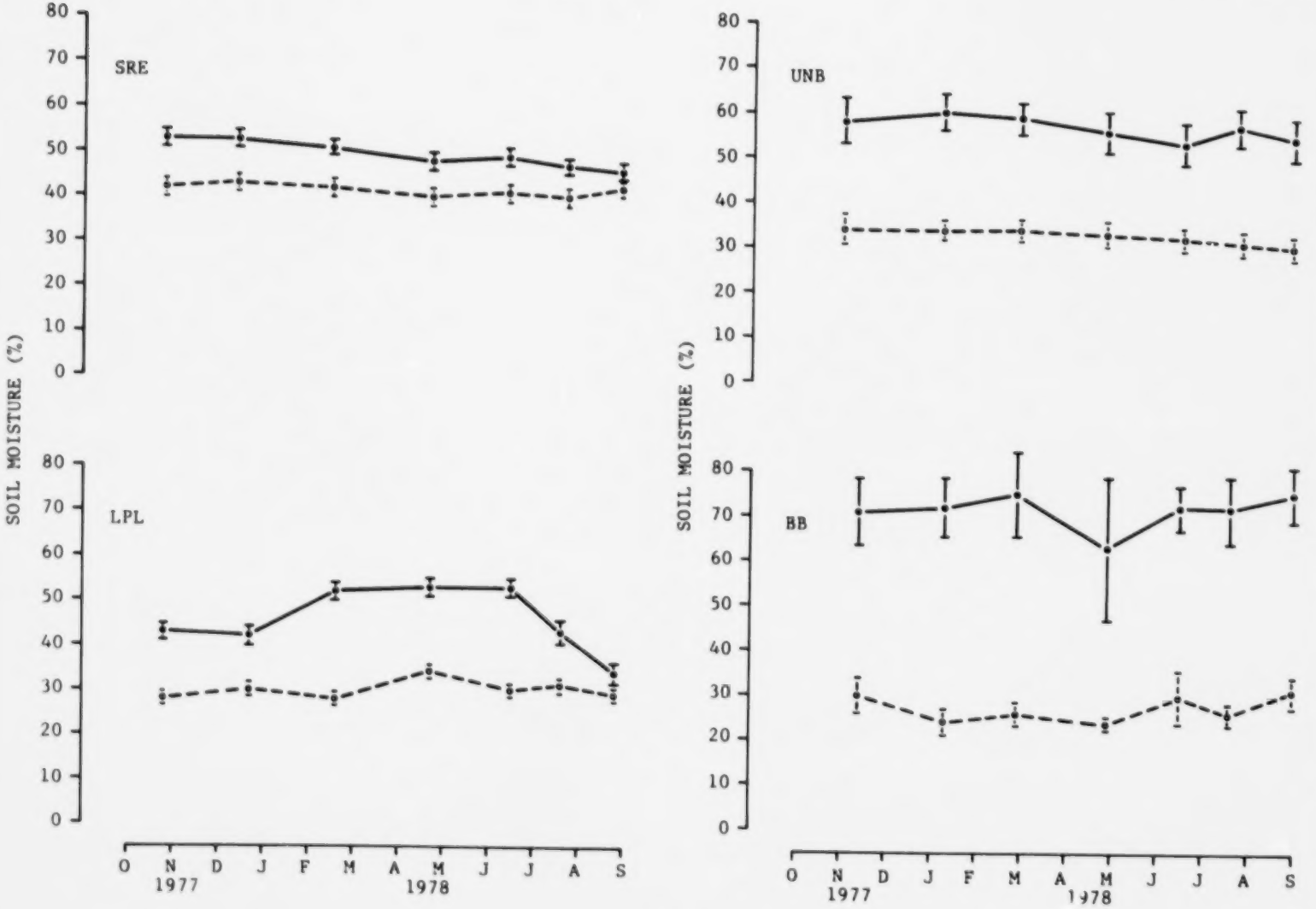

Figure 11. Mean water content (% of moist weight) of substrate at 0-5 cm (solid line) and 45-50 cm (dashed line) ± S.E. for study areas through the sample period.

Seasonal fluctuations in substrate water content, while not of great magnitude, were nevertheless apparent. Most macroplots and, indeed, most marsh harvest session means, showed minimums in the root zone during the summer and maximums between October and April. Sub-root zone water percentages followed the general pattern of root zone water content, but were less seasonally variable. Annual water content means suggested that Bolsa was wettest at the surface and driest below, and that Los Penasquitos was driest overall. Soil dryness at Los Penasquitos was revealed by surface cracks and, on many occasions, tremendous pressures were required to force the coring device into the soil substrate.

Temperature

Substrate temperature varied with time of year and depth (Appendices C.9 and C.10). The highest temperature recorded for the root zone was 27.8°C (UNB-7, session 7), for the sub-root zone 23.3°C (SRE-15, session 5). Minimums were 8.3°C (LPL-18, session 3) and 11.7°C (several macroplots at LPL, session 3) for root zone and sub-root zone, respectively. In general, the substrate was warmer in the summer than it was in the winter. Root zone temperatures exhibited a greater annual range than those at sub-root levels and, in most macroplots, annual means for the root zone were higher by about 1°C. However, with reference to harvest session means (Figure 12), it was clear that an annual pattern of temperature contrasts between the two levels was present. In December and January temperature increased with depth; little change of temperature with depth was present February to April, although the root zone tended to be somewhat cooler in the early part of this period then somewhat warmer than the sub-root zone in the latter part; June to July temperatures in the root zone were higher than those below; by October a shift to cooler root zone temperatures then those below was apparent.

Certainly variations in solar radiation through the year exert control on substrate temperatures, but temperature is also likely to be influenced by soil mositure from precipitation and tidal inundation and by foliar density of marsh plants.

Elevation

Sample macroplot elevations referenced to mean high water (MHW) ranged from -1.12 to 1.17 m (Appendix D). Most macroplots were located above MHW but, conspicuously, all macroplots at Bolsa were below this tide level (Figure 13). Because macroplots were positioned to represent the variety of vegetation patterns in study marshes, macroplot elevations provided a good approximation of the vertical range of salt marsh.

Habitat Type

Each macroplot was assigned to one of seven habitat types during the final field session (Appendix D). This classification represented a priori judgement and was not based on later knowledge of site production and analysis

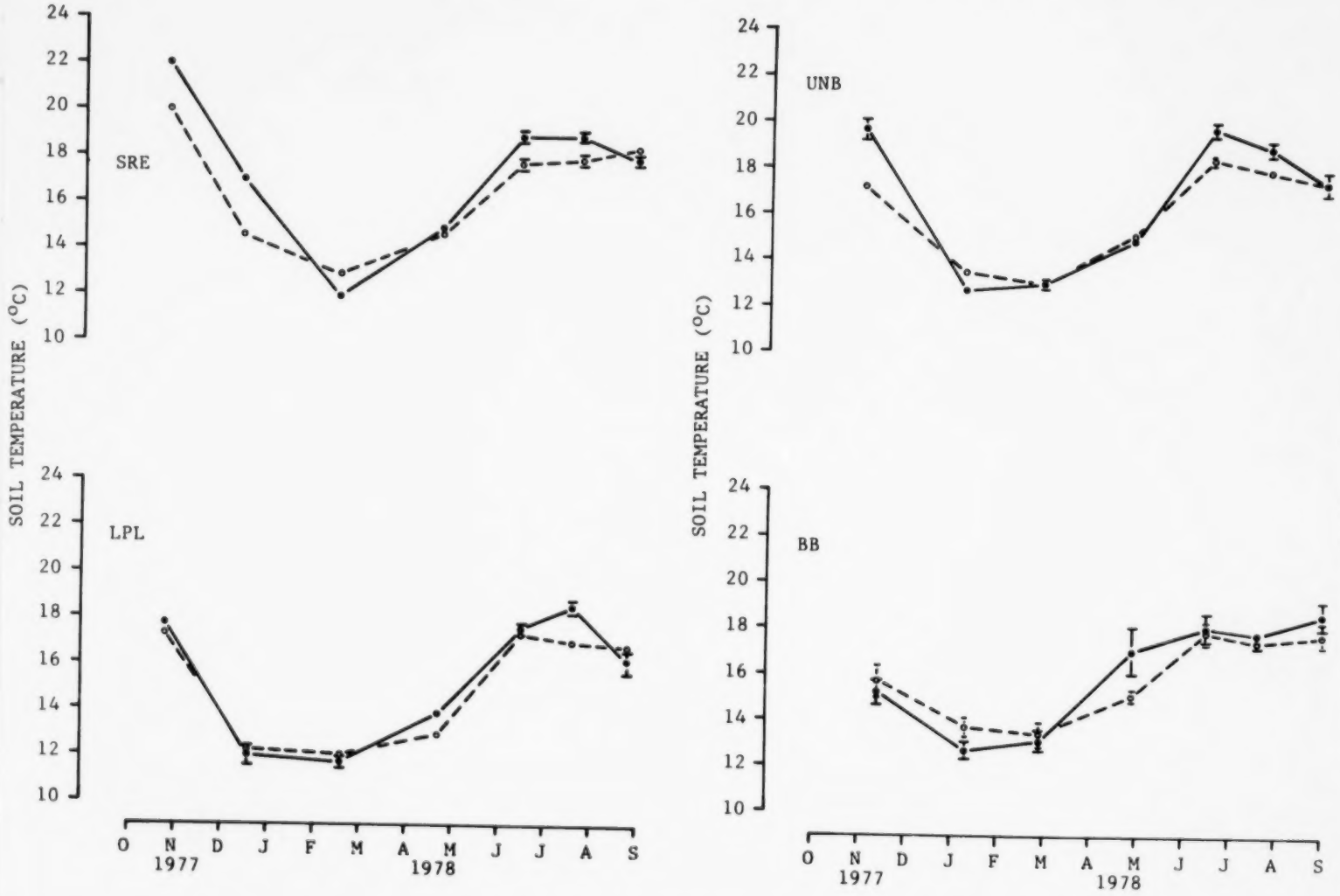

Figure 12. Mean temperature (°C) of substrate at 0-5 cm (solid line) at 45-50 cm (dashed line) ± S.E. for study areas through the sample period.

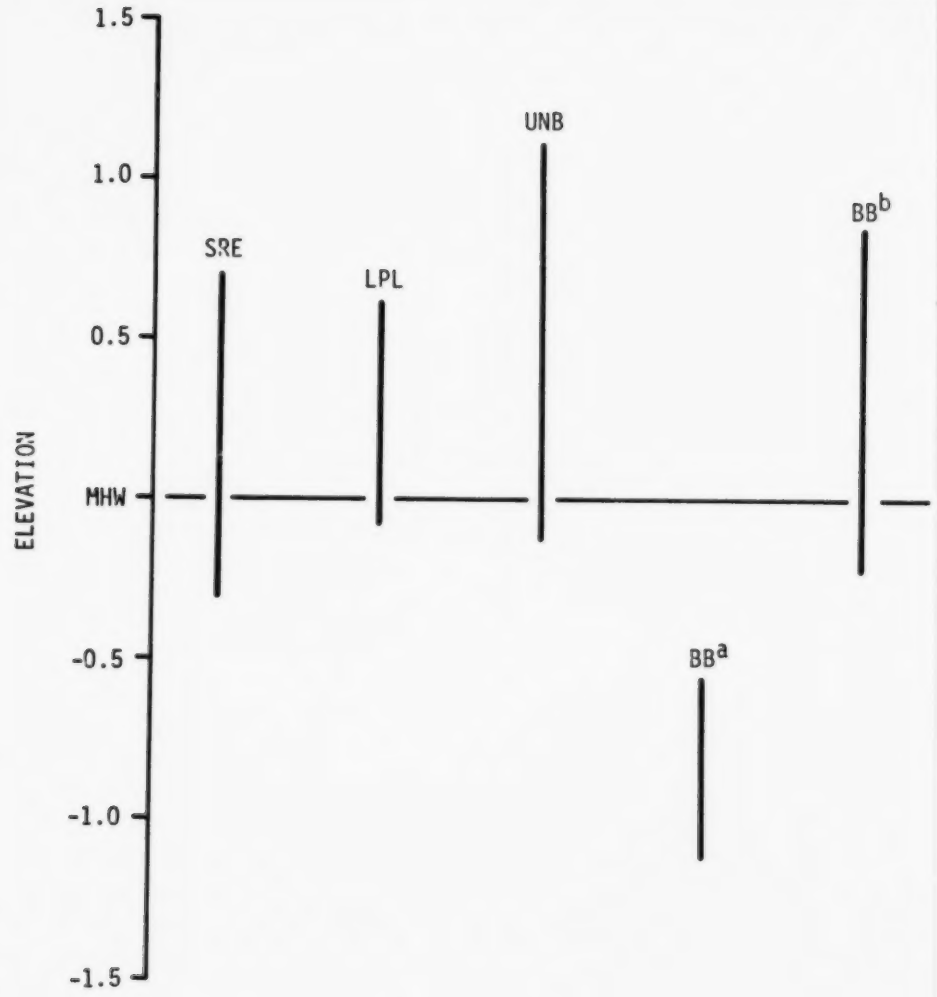

Figure 13. Vertical range of salt marsh in four southern California locations (m). SRE is Sweetwater River Estuary, LPL is Los Penasquitos Lagoon, UNB is Upper Newport Bay, BB[a] is Inner Bolsa Bay, BB[b] is Outer Bolsa Bay. Elevation in meters referenced to local mean higher water.

of seasonal trends in environmental variables. The distribution of habitat types along a hypothetical marsh profile is shown in Figure 14.

Fore Levee Slope (FLS)

Located adjacent to creeks and river channels and bounded on the upland side by a levee, the Fore Levee Slope habitat had the most intimate contact with tide waters and occurred at the lowest elevations (Table 9). Species diversity was low--usually only Spartina foliosa and, less frequently, Salicornia virginica and Salicornia bigelovii were present. At marshes with and without tidal fluctuation (Sweetwater and Newport versus Los Penasquitos and Bolsa), substrate salinity in this habitat fluctuated very little; most readings were near that of sea water. Redox potentials were generally low and, especially at Newport, often negative. The soil surface tended to heat rapidly by exposure to the sun at low tide.

Levee Crest (LC)

Levees along water courses were conspicuous in the field although they were often only 10 cm or less above adjacent marsh. This was often the site of vigorous growth in Salicornia virginica but, even at Los Penasquitos with its general low species diversity, multispecies stands were more common. Salinity extremes were greater here than in Fore Levee Slope, yet less extreme than other habitats. At Los Penasquitos mean salinity was lowest on levees. This habitat type was among the best drained; redox was high, soil water low, and ammonia low.

Back Levee Slope (BLS)

On the opposite side of the levee from Fore Levee Slope, and at higher elevations, Back Levee Slope extended away from water courses. This habitat was fairly well drained, generally high in species diversity, and the most widespread habitat at Sweetwater and Los Penasquitos. At Sweetwater mean root zone salinity was highest in Back Levee Slope. This habitat was universally low in ammonia.

Back Levee Depression (BLD)

Where water courses were well developed--Sweetwater, Los Penasquitos, Newport but not Bolsa--Back Levee Slope often ended in poorly drained shallow depression in which water remained on the surface for long periods after tidal inundation. Subsequent evaporation of impounded water in this habitat created high substrate salinity, especially at Los Penasquitos and Newport. Low redox values and high soil water content suggested persistent anaerobiosis. Ammonia levels were often high in this habitat, although not as high as those of Fore Levee Slope.

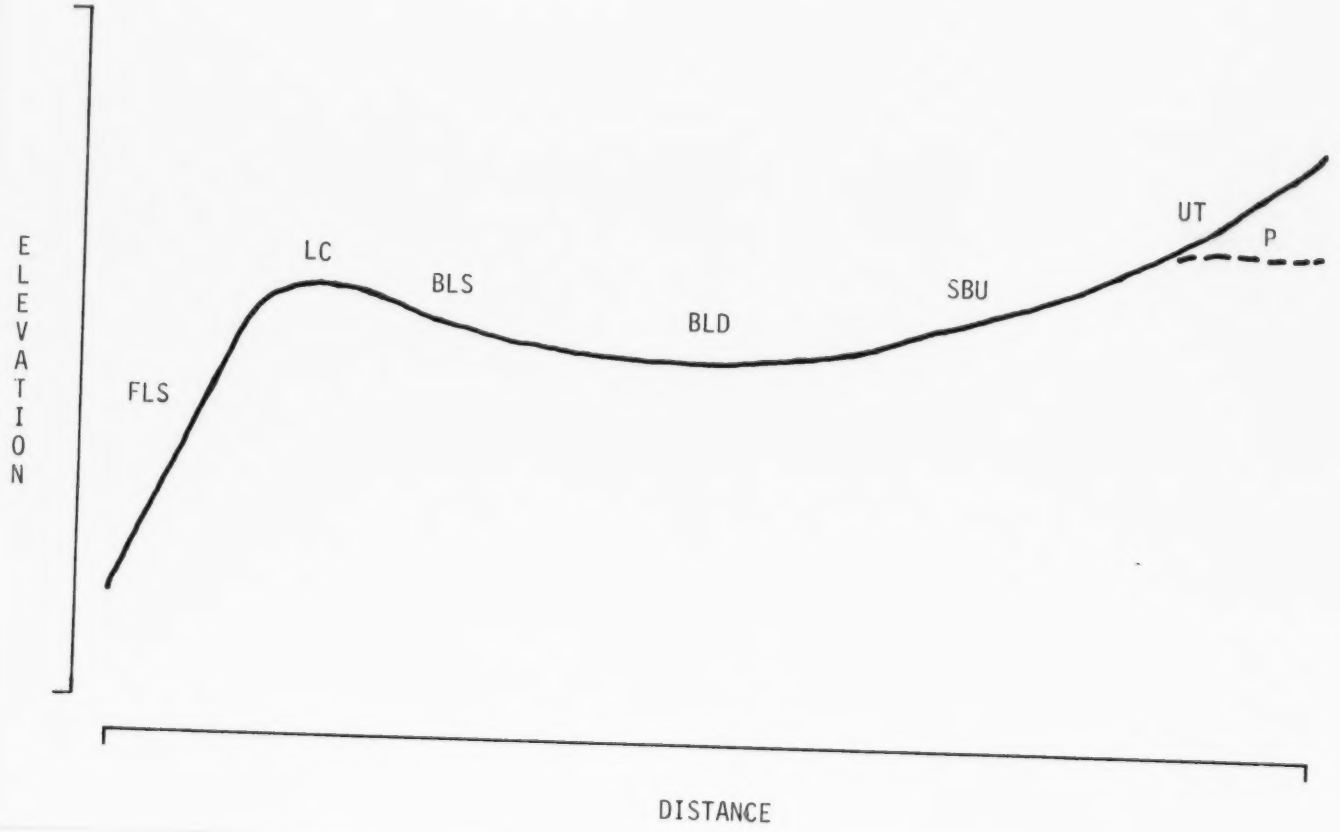

Figure 14. Location of habitat types along a hypothetical marsh profile. Habitats from left are Fore Levee Slope, Levee Crest, Back Levee Slope, Back Levee Depression, Slope Below Upland, Upland Transition, and Pan.

Table 9. Mean Elevation, Number of Species, and Substrate Conditions for Habitat Types

Marsh	Habitat	Elevation (m)	No. Species	Salinity (ppt)	pH	NH_3 (10^{-5}) M	Annual Mean Redox (Eh) mV	Soil Water (%)	Soil Temp. (°C)	n
SRE	FLS	-.25	2.0	40	6.5	2.6	340	44	18	3
	LC	.31	5.8	48	6.5	1.5	417	46	17	6
	BLS	.28	7.6	58	6.3	1.0	405	48	17	8
	BLD	.18	7.1	48	6.5	1.8	335	60	18	8
	SBU	.34	5.7	47	6.9	1.2	380	54	17	3
	UT	.48	2.0	44	7.0	1.7	384	39	17	2
	P	.52	1.0	90	6.9	.7	427	30	19	1
LPL	FLS	.21	1.0	39	6.9	2.2	342	48	16	1
	LC	.28	1.2	33	6.5	2.5	324	53	15	5
	BLS	.21	1.2	39	6.8	2.1	333	48	15	9
	BLD	.16	1.0	44	6.9	1.9	293	43	15	2
	UT	.49	2.3	39	6.5	2.5	366	34	16	4
UNB	FLS	.30	2.9	35	6.6	12.6	190	65	17	7
	LC	.54	6.0	38	6.7	1.7	321	52	16	2
	BLS	.50	8.0	38	6.3	1.0	333	69	16	4
	BLD	.65	6.6	58	6.1	3.5	300	71	17	7
	SBU	.77	9.0	39	7.2	1.0	344	23	16	3
	UT	1.11	2.5	33	8.3	1.0	352	9	18	2
BB	FLS	-1.10	1.5	41	7.3	24.0	-3	78	17	2
	SBU	-.91	3.0	29	7.3	6.3	102	80	15	2
	UT	-.57	2.0	20	7.0	3.3	208	53	15	1

Slope Below Upland (SBU)

Below the landward border, a sloping habitat--here labeled Slope Below Upland--often extended toward a water course or Back Levee Depression. Well drained and high in species diversity, this habitat type was generally low in ammonia and moderate in salt concentration.

Upland Transition (UT)

At the ecotone between marsh and upland, the most elevated habitat type--Upland Transition--was identified. High redox potentials and low root zone water content denoted good drainage. Relatively low salinity and moderate to low ammonia were characteristic. Species diversity at Los Penasquitos was highest in this habitat, but elsewhere the number of species was lower than might be expected. At Sweetwater and Bolsa, Frankenia grandiflora dominated this habitat; at Newport Monanthocloe littorlis and an occasional upland plant species (e.g., Lotus scoparius) were important; at Los Pensquitos upland transition was taken by a combination of Frankenia grandiflora, Distichlis spicata and Cressa truxillensis. Abnormally high pH in this habitat at Newport was most likely due to disintegration of shell in the substrate.

Pan (P)

Slight depressions at high marsh elevations collected water only from the highest tides. Through evaporation, expecially in the summer, salts were then concentrated and left at the surface. The Pan habitats were present in all four study marshes, but generally they contained little vascular plant life. At Sweetwater, however, a pan containing stunted growth of Salicornia virginica was sampled (SRE-15). Mean root zone salinity for this site was the highest recorded for all macroplots. Redox potential and root zone temperatures were high; ammonia and soil water were low. This habitat represents perhaps the most extreme marsh environment.

Net Production and Environment

Stand net production and elevation

Strength of the relationship between macroplot NAPP and elevation varied between study marshes (Figure 15). At Bolsa production increased dramatically with elevation ($R = .85$); relationships were positive but less dramatic at Los Penasquitos ($R = .55$) and Sweetwater ($R = .43$). No correlation between net production and elevation was detected at Upper Newport ($R = -.08$).

Species net production, elevation and plant communities

Plant species occupied marsh with certain elevational limits in study areas, and elevations of peak species production were generally unique (Figure 16). Moreover, vertical distribution of species and production peaks sug-

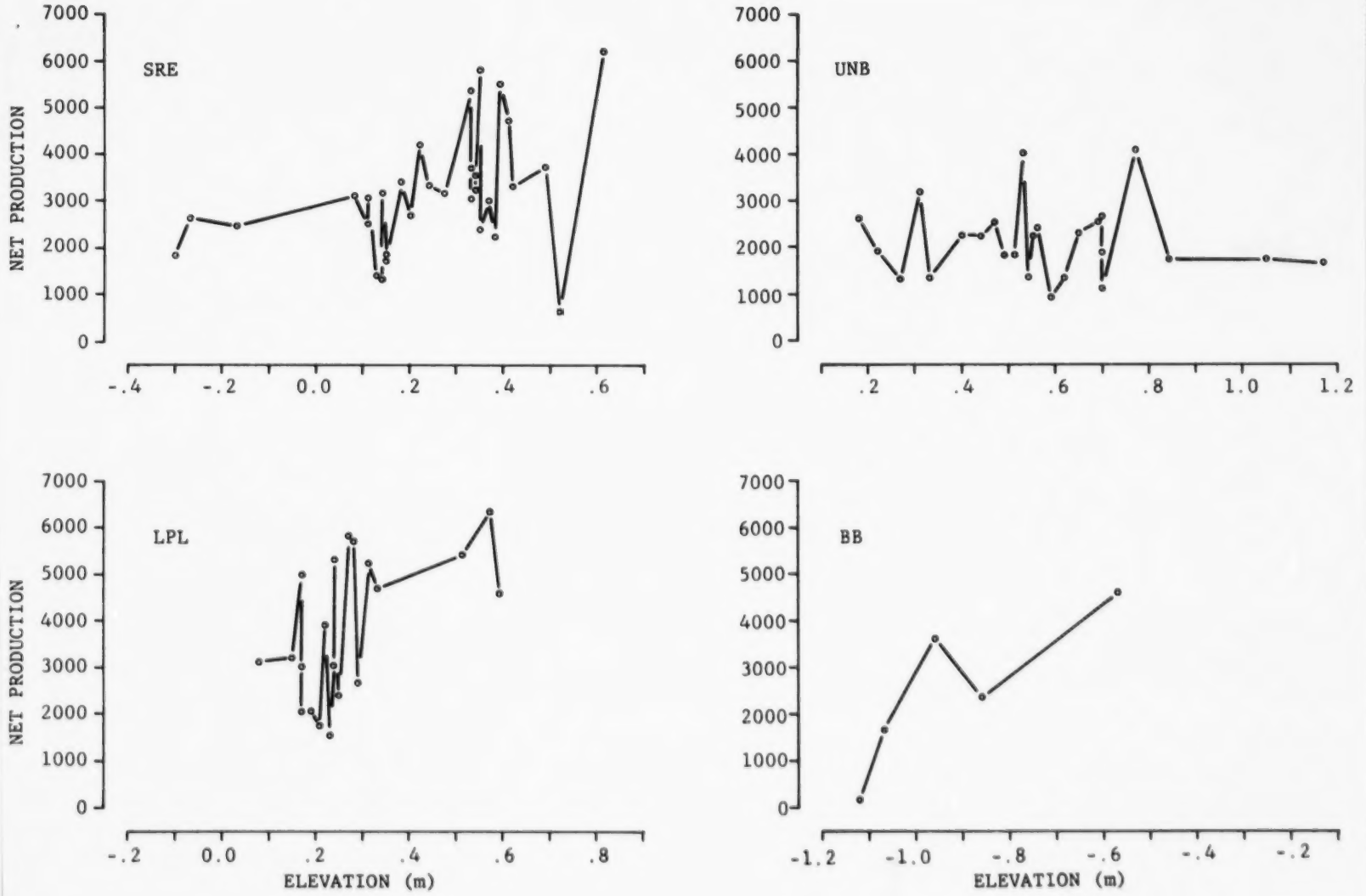

Figure 15. Macroplot net production and elevation. Production is SSTC in g $m^{-2}yr^{-1}$; elevation (m) referenced to local mean high water.

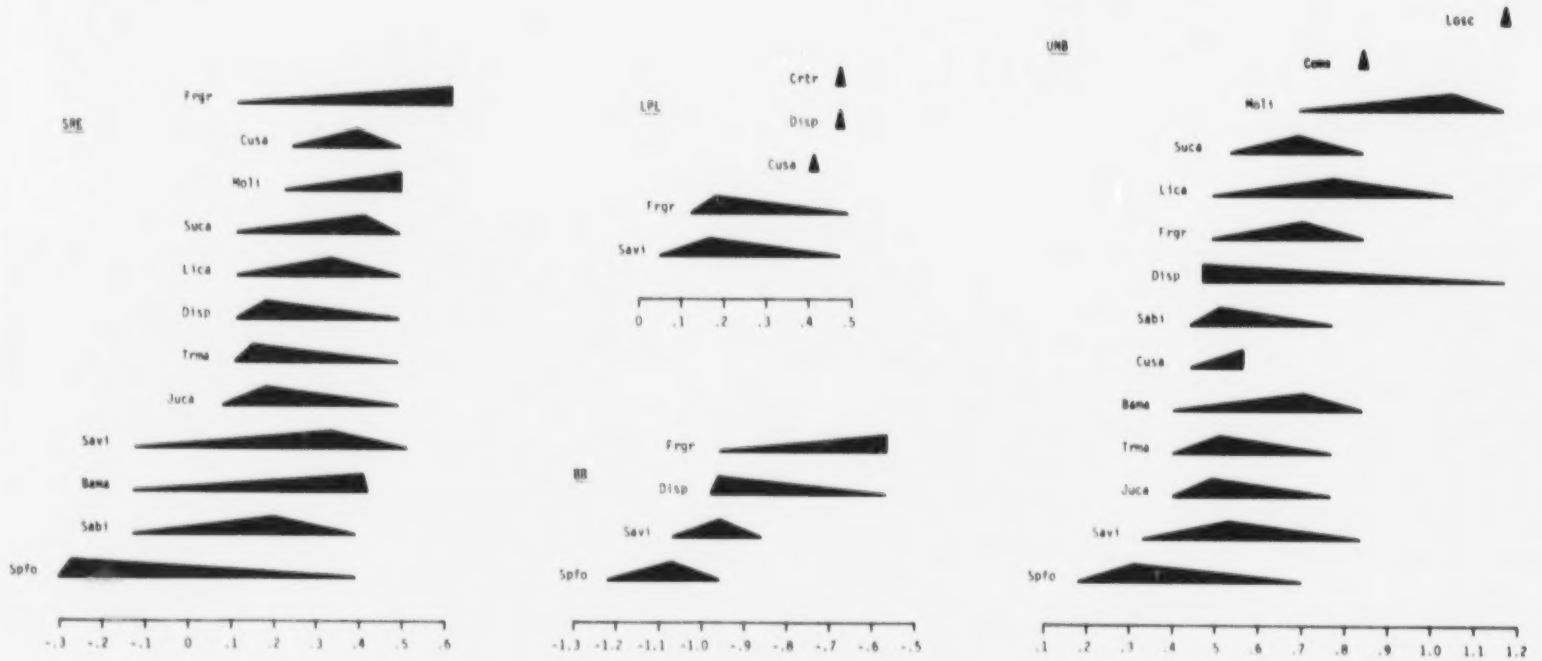

Figure 16. Elevational range of plant species in macroplot samples. Peak corresponds to elevation of maximum production. Elevation (m) referenced to local mean high water.

gested several plant communities along the elevation gradient in each marsh. At Sweetwater pure stands of Spartina foliosa extended to mudflat, but at elevations between -.1 and .1 m MHW, Spartina foliosa joined Salicornia virginica, Salicornia bigelovii and Batis maritima to form a multispecific community--Low Marsh. The High Marsh community at Sweetwater occurred between .1 and .5 m and was highly diverse; the Upland Transition community consisted of pure stands of Frankenia grandiflora above .5 m.

Communities similar to those present at Sweetwater occurred at Newport but with some notable exceptions. Spartina foliosa dominated the entire Low Marsh and Frankenia grandiflora did not constitute the Upland Transition. Instead Monanthocloe littoralis, Distichlis spicata and occasionally Limonium californicum occupied the highest levels.

Only High Marsh and Upland Transition communities were discernible at Los Penasquitos. Salicornia virginica and Frankenia grandiflora dominated the former; the latter was dominated by Frankenia grandiflora, Distichlis spicata and Cressa truxillensis.

Low Marsh, High Marsh and Upland Transition were present at Bolsa. Pure stands of Spartina foliosa comprised Low Marsh; Salicornia virginica and Distichlis spicata, with some Spartina foliosa and Frankenia grandiflora, inhabited High Marsh; Frankenia grandiflora and limited Distichlis spicata occurred in Upland Transition. Plant communities recognized in this study were essentially synonomous with the "low," "middle," and "high littoral" of other authors (Purer 1942, Vogl 1966).

That peak production for each species usually occurred at an elevation unique to the species supported the principle of competitive exclusion (Gause 1934) that I observed in an investigation of species-elevation relationships in Oregon salt marshes (Eilers 1976). But it should be noted that in both investigations arrayment of plant species along an abstract elevation gradient suggested abstract communities and, that in the field, the vegetation appeared more as a complex mosaic.

Stand net production and habitat type

Variation in production between habitats was significant ($P<.001$). Clearly two habitat types, Levee Crest and Upland Transition accounted for the greatest macroplot production (Figure 17). This suggested that good drainage and associated aerobic soils, moderate salinities, and moderate to low soil ammonia provided conditions associated with optimal plant growth. In contrast, Fore Levee Slope and Back Levee Depression showed the lowest mean production (with the exception of Pan habitat) and thus anaerobic substrate, high root zone water content, high soil salinity, and high ammonia were less supportive of high yield.

Back Levee Slope and Slope Below Upland habitats recorded moderate yield which was perhaps a reflection of moderate environmental conditions comprising these types. Of the two, however, Slope Below Upland tended to be the more productive; the difference was likely attributable to slightly higher eleva-

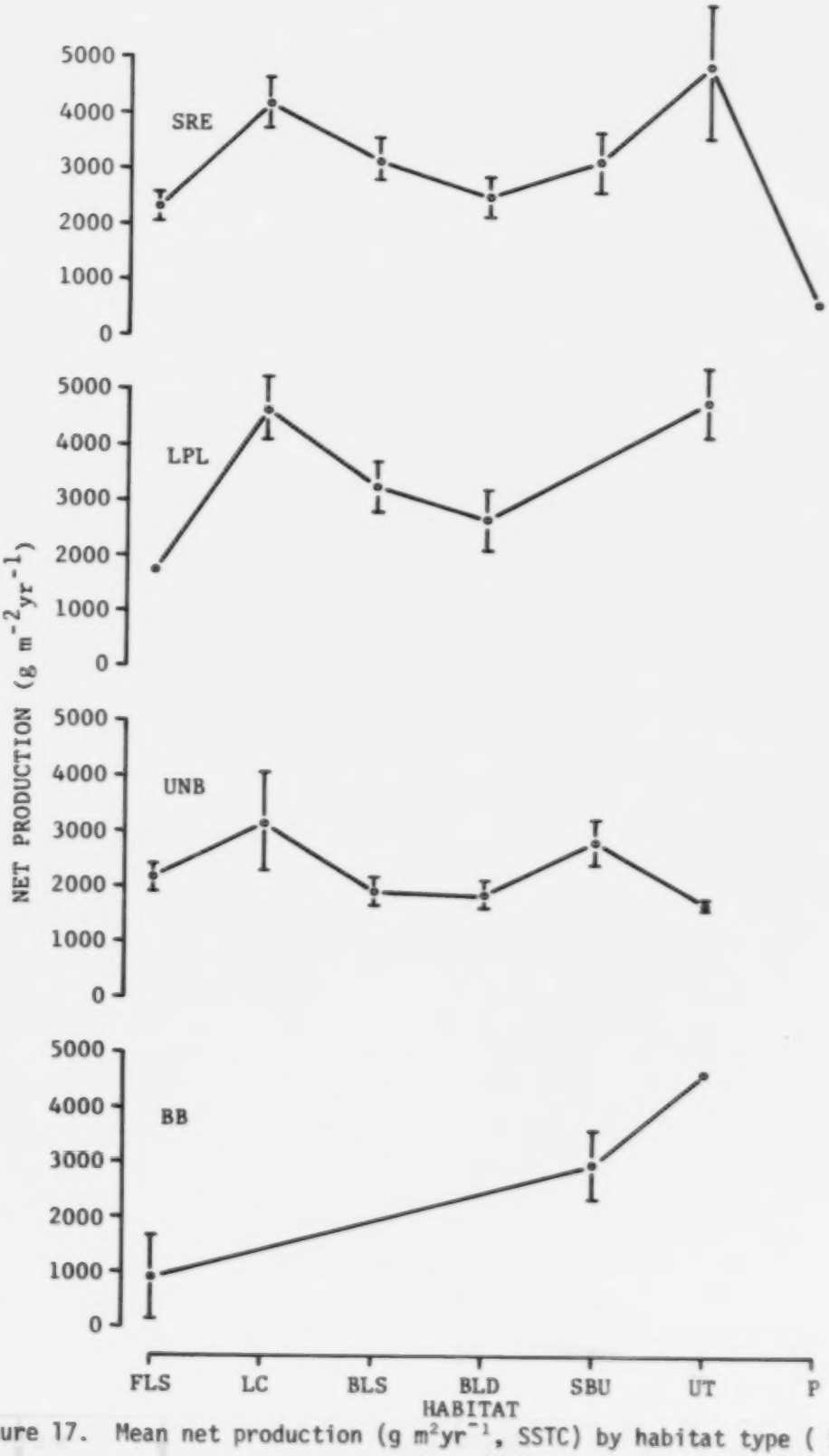

Figure 17. Mean net production (g m^2yr^{-1}, SSTC) by habitat type (S.E.).

tion in this habitat. Inhibitory effects of high salinity appeared to outweigh benefits of high elevation and good soil aeration in the Pan habitat type.

Species net production and habitat type

Even though most plant species occurred in more than one habitat type, each displayed maximum production and therefore maximum affinity to a particular type in each marsh (Table 10). Fore Levee Slope was favored by Spartina foliosa, and Salicornia bigelovii grew best in this habitat only at Sweetwater. Salicornia virginica achieved maximum production in Levee Crest where this habitat was available. Jaumea carnosa, Triglochin maritimum and Cuscuta salinia did best in Back Levee Slope and Back Levee Depression; Batis maritima produced at maximum in Back Levee Depression at Newport and Slope Below Upland at Sweetwater. Peak production of Limonium californicum and Suaeda californica occurred in Slope Below Upland.

Habitat affinities of several species varied from one marsh to the next. Most curious in this regard was Frankenia grandiflora. Upland transition was its most productive habitat at Sweetwater and Bolsa; at Los Penasquitos, while more productive in Back Levee Slope, it produced high yields in Upland Transition. However, at Newport, its maximum growth (a low 134 g $m^{-2}yr^{-1}$) occurred in poorly drained Back Levee Depression habitat. Two explanations were possible. Competition with Monanthocloe littoralis may have excluded Frankenia grandiflora from Upland Transition at Newport, or perhaps, coarse grained substrate there favored Monanthocloe littoralis but did not retain enough moisture for establishment of Frankenia grandiflora. At any rate, the low production of Frankenia grandiflora at Newport merits further investigation. Distichlis spicata displayed the greatest variation in habitat affinity; it achieved maximum production in a different habitat in each study marsh.

From the foregoing it was clear that, while for some species maximum production always occurred in the same habitat or closely related habitats (e.g., Spartina foliosa, Jaumea carnosa), peak production for other species (e.g., Distichlis spicata) was prone to intermarsh variability.

Explanatory models: net production and environment

Pearson correlation coefficients which indicate the degree to which two variables covary were computed for NAPP (as SSTC) with macroplot elevation, number of species, and annual values (mean, minimum, maximum and range) for substrate variables (Table 11). On the strength of coefficients, eight independent variables were selected for stepwise multiple regression analysis as noted in the table. Table 12 resulted from the initial analysis. For Sweetwater, root zone temperature entered the regression equation on the first step with a significant R^2 of .54. The addition of root zone water content, root zone salinity, elevation, and free water ammonia on successive steps created a regression model that explained 72 percent of the observed variation in macroplot production. Subsequent steps did not add to the model. Salinity

Table 10. Mean Species Net Production for Habitat Types (g $m^{-2}yr^{-1}$)

Marsh	Species	Habitat						
		FLS	LC	BLS	BLD	SBU	UT	P
SRE	Bama		96	151	215	919		
	Cusa		2	238	74	28		
	Disp		238	443	78			
	Frgr		773	488	137	698	4838	
	Juca		104	465	981			
	Lica		288	68	157	476		
	Moli		303	241	49			
	Sabi	458		182	330	3		
	Savi	1122	2196	1048	810	1020	131	665
	Spfo	2034	3	166	175			
	Suca		149	83	97	363		
	Trma		43	166	178	197		
LPL	Crtr						127	
	Disp						1184	
	Frgr		2574	3347			3459	
	Savi	1767	4006	2499	2636		1585	
UNB	Bama	155	198	81	509	45		
	Coma					8		
	Cusa	1			5			
	Disp		780	444	70	152	401	
	Frgr		27	14	134	101		
	Juca	284	96	392	184	88		
	Lica		3	67	57	522	357	
	Losc						5	
	Moli				6	969	1175	
	Sabi	1	1	223	67	1		
	Savi	324	1980	175	764	357		
	Spfo	1661	50	52	194			
	Suca		16			155		
	Trma	63	261	352	187	53		
BB	Disp					891	74	
	Frgr					72	4564	
	Savi	459				1323		
	Spfo	598						

Table 11. Pearson Correlation Coefficients for NAPP with Elevation, Number of Species and Substrate Variables. Variables Selected for Regression Analysis are Indicated.

Variable		SRE	LPL	UNB	BB	ALL
Elevation [a]		.43	.55	-.08	.85	.07
Number of Species [a]		.13	.51	.02	.60	.09
Salinity	$\bar{x}$[a,b]	-.30	-.53	-.39	-.79	.27
	min.	-.17	-.24	-.32	-.76	-.19
	max.	-.27	-.19	-.18	-.41	.06
	range	-.20	-.15	-.02	.62	.13
pH	$\bar{x}$[a]	.10	-.45	.07	-.70	-.06
	min.	.01	-.28	.02	-.79	-.08
	max.	.01	-.31	.24	-.37	-.04
	range	-.12	-.07	.34	.09	.01
NH_3	$\bar{x}$	-.10	-.38	-.03	-.57	-.26
	min. [a]	.17	-.32	-.19	.19	-.19
	max.	-.18	-.38	.09	-.86	-.25
	range	-.18	-.38	.09	-.86	-.25
Redox	$\bar{x}$	.45	.05	.04	.70	.30
	min. [a]	.45	.32	.26	.74	.37
	max.	.23	-.03	.21	.37	.18
	range	-.27	-.38	-.16	-.86	.39
Soil Water	$\bar{x}$[a,b]	-.19	-.14	-.19	-.54	-.32
	min.	-.29	-.12	-.25	-.48	-.38
	max.	-.03	-.20	-.17	-.51	-.19
	range	.38	.03	.34	.40	.31
Temperature	$\bar{x}$[a,b]	-.74	-.08	-.66	-.73	-.42
	min.	-.46	.31	.01	-.68	-.38
	max.	-.13	-.38	-.45	-.85	-.24
	range	.18	-.49	-.37	-.93	-.11

[a] Selected as independent variables for regression analysis.
[b] Root zone

Table 12. Summary of Stepwise Multiple Regression--NAPP with Elevation; Number of Species; Root Zone Salinity, Water Content, and Temperature; and Soil Free-Water Ammonia, Redox and pH.

	Step	Variable Entering	Multiple R	R^2	Simple R
SRE	1.	Temp	.74	.54	-.74
	2.	Water	.76	.58	-.19
	3.	Salt	.79	.62	-.30
	4.	Elev	.83	.68	.43
	5.	NH_3	.85	.72	.17
	6.	Species	.85	.72	.14
	7.	Redox	.85	.72	.45
LPL	1.	Salt	.53	.28	-.53
	2.	Spp	.73	.54	.51
	3.	Elev	.78	.61	.55
	4.	Temp	.79	.63	-.08
	5.	Water	.79	.63	-.14
	6.	Redox	.79	.63	.32
	7.	pH	.79	.63	-.45
	8.	NH_3	.79	.63	-.32
UNB	1.	Temp	.70	.49	-.70
	2.	Water	.74	.54	-.23
	3.	Salt	.75	.56	-.39
	4.	Species	.77	.60	.00
	5.	Redox	.78	.61	.26
	6.	NH_3	.79	.62	-.20
	7.	pH	.79	.63	.15
	8.	Elev	.79	.63	-.01
BB	1.	Elev	.85	.73	.85
	2.	Species	.99	.98	.60
	3.	Water	.99	.99	-.53

entered the equation first for Los Penasquitos (R^2 = .28) followed by species and elevation. The three variables together accounted for 61 percent of the variation in production; continuation of the stepwise process added little. Temperature was again the first independent variable to enter for Newport (R^2 = .49) and, on the next step, it was joined by root zone water content to explain 54 percent of NAPP variation. Addition of the remaining variables increased the explanation by small increments to 63 percent. Elevation and number of species provided a strong combined R^2 of .99 for Bolsa, but soil water content was the only additional variable to enter and it added little.

Analysis to this point suggested that high root zone temperature was an important constraint on NAPP in tidally controlled marshes. It might be expected that more frequent inundation at lower elevation moderates temperatures, yet the correlation between mean root zone temperature and elevation at Sweetwater was strongly negative ($R = -.67$). At Newport, however, this correlation was moderately positive ($R = .23$) and supportive of a tide-temperature relationship. A check of mean temperatures recorded for Newport macroplots revealed that those contributing most to the positive correlation were located on old dredge spoil and thus this apparent positive relationship should be approached cautiously. Furthermore, the question of temperature modification by marsh plants needed to be considered. It was reasoned that high production should correlate well with low root zone temperature because of shading by high foliar density and, therefore, high production itself could be partially responsible for lower soil temperature. Inclusion of number of species was also questioned because, as a vegetation characteristic, its presence in the analysis would not help to explain variation in NAPP in terms of environmental factors.

With these considerations in mind, temperature and number of species were excluded from the independent variables and regression models recomputed (Table 13). Redox, elevation, and root zone salinity combined in a new model for Sweetwater to explain 56 percent of NAPP variation; addition of NH_3 and water content of the root zone increased the R^2 to .66. The combination of salinity, elevation, NH_3, salinity, and pH produced $R^2 = .56$ at Los Penasquitos. Salinity and redox were most important (combined $R^2 = .26$) at Newport, but the expansion of the regression equation to include elevation, soil water, and pH increased the R^2 by .11. Elevation, soil water and soil salinity entered the equation for Bolsa ($R^2 = .99$). Treatment of all marshes together produced a combined R^2 for redox and salinity of .29, but further addition of variables did not improve the multiple R^2.

A combination of variables provided at least a partial explanation of NAPP variation in each study marsh, but variables related to soil aeration and waterlogging (redox, soil water content, and, in some ways, elevation) and soil salinity were consistently important constraints on production. The models suggested that high production was most likely to occur at well-drained, aerated, low-salinity locations (such as Levee Crest and Upland Transition habitats) and that low production could be expected in sites where water collects on the marsh and remains for long periods (Back Levee Depression and Fore Levee Slope habitats). Low production could also be expected where elevated soil salinity results from evaporation of surface water (Back Levee Depression at Los Penasquitos and Newport and Pan at Sweetwater). Production was apparently not limited by nitrogen (NH_3) as suggested by Valiela and Teal (1974). Only in the regression model for Sweetwater did a positive relationship with ammonia occur.

Strength of regression models varied between marshes, but the general levels of explanation for differences in macroplot production were high and significant (all $\leq .14$). A search for the source of unexplained variation in production ($1 - R^2$) through computation and graphic presentation of residuals to each model produced no consistent patterns. Perhaps the inherent variability of marsh vegetation and limitations imposed by sampling each time at a

Table 13. Summary of Stepwise Multiple Regression--NAPP with Elevation; Number of Species; Root Zone Salinity, Water Content, and Temperature; and Soil-Free Water Ammonia, Redox and pH.

	Step	Variable Entering	Multiple R	Multiple R^2	SimpleR
SRE	1.	Redox	.45	.21	.45
	2.	Elev	.59	.36	.43
	3.	Salt	.75	.56	-.30
	4.	NH_3	.78	.62	.17
	5.	Water	.81	.66	-.19
	6.	pH	.81	.66	.10
LPL	1.	Salt	.53	.28	-.53
	2.	Elev	.69	.47	.55
	3.	NH_3	.71	.50	-.31
	4.	Water	.72	.52	.32
	5.	Redox	.75	.56	.32
	6.	pH	.75	.57	-.45
UNB	1.	Salt	.39	.15	-.39
	2.	Redox	.51	.26	.26
	3.	Elev	.53	.28	-.01
	4.	Water	.56	.31	-.28
	5.	pH	.61	.37	.14
BB	1.	Elev	.85	.73	.85
	2.	Water	.93	.87	-.54
	3.	Salt	.99	.99	-.79
All	1.	Redox	.37	.14	.37
	2.	Salt	.54	.29	-.27
	3.	NH_3	.54	.29	-.19
	4.	pH	.54	.29	-.06
	5.	Water	.55	.30	-.32
	6.	Elev	.55	.30	.07

different position within macroplots were factors. Other variables not included in this investigation (such as soil texture, soil nutrients other than ammonia-N, water table depth, and animal trampling and herbivory) could have provided additional explanation.

DISCUSSION

Disappearance of Dead Material

The rate at which dead material disappears from the marsh is closely related to several factors including temperature, precipitation, tides, and the organic nature of marsh plants (Kirby and Gosselink 1976). Rates could be expected to vary with seasons and with the mix in species composition as was observed in this study. Wiegert and Evans (1964) suggested two methods--litter bags and paired plots--by which to estimate the disappearance of dead material and applied each in a study of old field vegetation in Michigan. Subsequently, several authors applied one or the other of these techniques to investigations of salt marshes along the Atlantic and Gulf Coasts of North America. The range of their estimates, those of Wiegert and Evans (1964), and estimates generated by this study are presented in Table 14. Disappearance rates for southern California marshes compare closely to those obtained by the litter bag technique elsewhere, but litter bag estimates are, in general, lower than values obtained by utilization of paired plots. Litter bags exclude larger detritivores and retard water movement that might otherwise remove dead material (Hopkinson et al. 1978). The paired plot technique is more sensitive to tidal deposition and removal of dead material and to consumer activity. Therefore, paired plots are likely to approximate decomposition under natural conditions better than the litter bag methods. Thus, even though disappearance rates determined by the litter bag technique provide insight into the decomposition process and allow adjustments to dead biomass for computation of NAPP, resultant production is probably somewhat underestimated by this method.

Net Production

Role of tidal fluctuation

The importance of tidal action to nutrient cycling and production in salt marshes is well recognized (Odum 1961, Teal 1962, Steever et al. 1976) and most, if not all, previous investigations have been confined to salt marshes with unrestricted tidal access. The inclusion of Los Penasquitos and Bolsa in this study allows comparison of production with and without regular tidal control. It appears that in southern California, salt marsh macrophyte production may be helped by restricted tidal contact. Mean production at Los Penasquitos was 1.3 to 1.6 times greater than that at Sweetwater and 1.9 to 2.2 times greater than Newport (based on ST and SSTC values). Waterlogging reduced production at Bolsa and the anomalously low level of the marsh there prevents direct comparison with Los Penasquitos or other sites, but it may be noted that production of macroplot BB-1 was above that of all Newport sites

Table 14. Disappearance Rate of Dead Material in Michigan and Salt Marshes along the Atlantic and Gulf Coasts of North America Compared to Salt Marshes in Southern California (mg $g^{-1}day^{-1}$). The Range of Values Contain Means for Plant Species Sampled.

Source	Locale	Method	
		Litter Bags	Paired Plots
Wiegert and Evans (1964)	Michigan	.3 - 4.6	1.3 - 13.6
Linthurst and Reimold (1978)	Maine to Georgia		.1 - 34.8
Odum and de la Cruz (1967)	Georgia	1.2 - 3.1[a]	
Kirby and Gosselink (1976)	Louisiana	4.9 - 6.3[a]	
White et al. (1978)	Louisiana	1.7 - 3.2	
Hopkinson et al. (1978)	Louisiana		4.0 - 18.9
This Study	California	.7 - 3.7	

[a] Spartina alterniflora only.

and above the mean for Los Penasquitos. Conditions in the lagoon are perhaps near ideal for growth of Salicornia virginica and Frankenia grandiflora; elsewhere both exhibit greatest vigor in well-drained levee and high marsh sites with infrequent inundation. Tidal access to Los Penasquitos is restricted to winter and spring months when the marsh is less photosynthetically active. Lack of tidal fluctuation may further support high production in Salicornia virginica and Frankenia grandiflora by reduction of species diversity.

Nearly all plants recorded in all sample macroplots occurred at Sweetwater and Newport, and polyspecific stands were very common in both. Monospecific stands characterized Los Penasquitos and Bolsa, and the total flora recorded from these sites was limited to five and four species, respectively. Furthermore, the mean disappearance rate of dead material at Los Penasquitos was 1.3 times lower than that for Sweetwater and 1.5 times lower than that for Newport. This implies that nutrient cycling at Los Penasquitos is retarded in comparison to tidally controlled sites; but higher production, larger litter accumulation, and infrequent inundation at Los Penasquitos suggests that nutrients tend to remain on site and benefit marsh plants rather than estuarine organisms as is likely to be the case with regular tidal flushing.

Elevation versus habitat

In an earlier investigation of an Oregon coastal salt marsh (Eilers 1979), I observed an increase in macrophyte production with elevation, but production in certain sites such as creek levees and back levee depressions did not conform to the general gradient pattern. Little reference to production ecology appears in the literature, but numerous authors who have studied Atlantic and Gulf Coast marshes report higher production of Spartina alterniflora on creek banks than in inland areas (for example, Smalley 1959, Kirby and Gosselink 1976). Brereton (1971) found that Salicornia grew with greatest vigor in aerated soils; Puccinellia maritima performed best in waterlogged soils. This leads to the question of the relative importance of elevation and habitat in terms of production levels. The current investigation of southern California marshes sheds some light on this question. It appears that the strength of the relationship between production and tide levels depends on the marsh under consideration. A very strong positive relationship occurred at Bolsa, no relationship was detected at Newport, and a moderately positive relationship was observed at Los Penasquitos and Newport. Winfield and Zedler (1976) found a parabolic relationship between net production and elevation classes in salt marshes of the Tijuana River Estuary (southern California) with the dip at mid-elevations. Mahall and Park (1976a) recorded minimum production at the Spartina-Salicornia ecotone in San Francisco Bay. To relate production to elevation alone may, therefore, produce conflicting results. As this investigation suggests, production in salt marsh vegetation is more tuned to a combination of environmental factors--soil water content, redox potential, salinity, inundation period, and elevation--than to an abstract elevation gradient alone. Indeed, elevation controls inundation period, but microtopography and soil texture control drainage. The degree of drainage in turn influences soil aeration, salinity, redox potential, pH and nutrient levels. At any given elevation, several different habitats--each composing a different combination of environmental variables--may occur. Back levee depressions may be found at the same absolute elevation as levee segments, and intramarsh Pan may occur at the same elevation as Upland Transition. Furthermore, microtopography may be influenced by tide level to create strongly contrasting habitats. Poorly drained areas at low elevation--Back Levee Depressions--are perpetually waterlogged, but frequent tidal inundation prevents extreme salt concentrations. Infrequent tidal flooding of elevated depressions--Pan habitat--leads to very high salt concentrations in the soil root zone through prolonged evaporation, but soils are generally not waterlogged and redox potentials are high. It appears, then, that habitat exerts greater control over production of salt marsh vegetation than does elevation (and tidal inundation) alone. This suggests that if a strong relationship between production and elevation is observed, as at Bolsa, the various habitats are not fully represented and/or the spatial arrangement of habitats supports the production-elevation relationship. Creek levees and Back Levee Depressions are not present at Bolsa and, because soil salinity and waterlogging decrease sharply with increased elevation, the strong positive relationship is not surprising. The weak production-elevation relationship at Newport attests to the occurrence of contrasting habitats (and hence different levels of production) at similar elevations.

Comparison with other salt marshes and latitudinal trends

Reported studies of production in salt marshes along the Pacific Coast of North America are scarce, and thus a comparative treatment is difficult. The task if further complicated by the lack, as Kirby and Gosselink (1976) found when they sought comparisons for their work in Louisiana, of uniformity in methodology among studies. Table 15 brings these reported studies together and comparisons, at least among estimates derived by similar methods, are possible. Production in the four southern California marshes studied is from 1.5 to 2.8 times greater than that of Nehalem Bay. This is not unexpected because production in Oregon is confined to the warm months, and aerial portions die back to ground level each fall.

That all four marsh estimates (SST) from this study are well above values computed for Tijuana River Estuary by Zedler and Maurillo (1979) is curious. Sweetwater is located closest to Tijuana; they are similar in species composition and setting (estuaries with some fresh water inflow), but production in monospecific stands of Spartina foliosa is 2.5 times greater at Sweetwater (2033 versus 832 g $m^{-2}yr^{-1}$). Steever et al. (1976) found that production of Spartina alterniflora in Connecticut marshes increases with tidal range. Spartina foliosa is the ecological equivalent of Spartina alterniflora in California marshes. Tide range (MLLW to MHHW) at Sweetwater is 1.8 m; tide range at Tijuana has not been published. However, the National Ocean Survey has operated a tide recording station on the municipal pier at Imperial Beach since 1971. The pier extends into the Pacific Ocean 2.5 km northwest of the entrance to Tijuana Estuary, and tide range there is 1.6 m--very close to that at Sweetwater. Warme (1971) reported poor establishment of Spartina foliosa at Mugu Lagoon where tidal range is reduced to .4 m by a sill of accumulated sand at the lagoon entrance. The disparity in production levels for Spartina (and perhaps other species) between Sweetwater and Tijuana suggests that a reduced tidal range similar to that at Mugu Lagoon is present at Tijuana. There could also be differences in method between the two studies that are not apparent. Obviously, more research into this matter is needed.

Zedler and Mauriello's (1979) production estimate of 2792 g $m^{-2}yr^{-1}$ for pure stands of Salicornia virginica at Los Penasquitos in 1978 is close to pure stand mean of 3062 g $m^{-2}yr^{-1}$ (SST) produced by this study. This level of production Los Penasquitos may not, however, be achieved every year for Zedler and Mauriello (1979) reported Salicornia virginica growth in July-August 1978 to be 2.4 times that of 1977 for the same period. They contend that greater rainfall and partial impoundment of runoff due to late spring entrance closure in 1978 are responsible for the disparity. This interpretation is open to question. I observed water levels in June 1977 to be .4 m higher than in June 1978 (entrance closed at both times) and, while 1978 was indeed the wetter year, August 1977 was one of the wettest on record (NOAA 1977, 1978). This suggests that prolonged inundation of the marsh in late spring and summer 1977 held July-August production to an abnormally low level and that high production returned with the more favorable inundation-moisture balance of 1978.

Because production estimates of Eilers (1979), Hoffnagle et al. (1976) and those of this study are based on nearly identical methodology, some

Table 15. Net Production for Salt Marshes Along the Pacific Coast of North America (g $m^{-2}yr^{-1}$)

Source	Locale	Production	Method
Burg et al. (1975) Washington	Puget Sound	750[a], 90-1400[b]	Max.-min. live standing
Eilers (1979) Oregon	Nehalem Bay	1400[a], 227-2800[b]	SST[g]
Hoffnagle et al. (1976) Oregon	Coos Bay	380-1100[b]	SST
Cameron (1972) California	San Francisco Bay	1200[c]-1700[c]	Peak live standing crop
Mahall and Park (1976a) California	San Francisco Bay	960[c], 690[c]	Peak live standing crop
This Study California	Bolsa Bay	2494 (2368)[a]	SSTC[h] (SST)
Upper Newport Bay California		2150 (2034)[a]	
Los Penasquitos Lagoon California		3787 (3539)[a]	
Sweetwater River Estuary California		3196 (2943)[a]	
Zedler and Mauriello (1979) California	Los Penasquitos Lagoon	2792[c] in dead standing crop	Increase in live + increase
Mission Bay California		544[c]	
Tijuana River Estuary California		832[d], 971[e], 944[f]	SST

[a] Marsh mean
[b] Community means
[c] Salicornia virginica mean
[d] Spartina foliosa mean
[e] Middle marsh mean
[f] High marsh mean
[g] Method of Smalley (1959) applied to species with summation of species production.
[h] SST corrected for losses due to disappearance of dead material.

observations on latitudinal trends in production along the Pacific Coast are possible. I suggested earlier (Eilers 1979) that salt marsh production might be expected to decrease with decreasing latitude as summer aridity increases soil salinity. While maximum soil salinity in Oregon marshes (Eilers 1975) is 3 to 10 times less than that observed in this study, net production based on marsh means is 1.5 to 3.0 times greater in southern California. It appears that summer drought and increased soil salinity at lower latitudes are more than compensated for by the warm temperatures and high light levels that promote a year-long growing season. But these observations are tentative at best. Clearly, more work and a convergent methodology are needed before latitudinal trends in production along this coast can be firmly established.

Turner (1976) reviewed and, in some cases, recalculated estimates of macrophyte production in salt marshes of the Atlantic and Gulf Coasts and observed an increase in production with decreasing latitude. Comparsion of estimates recalculated by the Smalley (1959) method with those of this study suggest that marsh production in southern California is close to, if not greater than, that of similar latitudes. For example, net production of tall Spartina alterniflora in Mississippi is 1964 g $m^{-2}yr^{-1}$ (de la Cruz 1974 in Turner 1976); the ST mean for all pure stands of Spartina foliosa sampled at Sweetwater and Newport is 2051 g $m^{-2}yr^{-1}$. Kirby and Gosselink (1976) estimated net production of Spartina alterniflora on creek banks and inland sites in Louisiana coastal marsh at 2645 and 1323 g $m^{-2}yr^{-1}$, respectively, using the method of Wiegert and Evans (1964). The comparable SSTC mean for pure stands of Spartina foliosa (2272 g $m^{-2}yr^{-1}$) is near the creek bank value, but mean production for this study based on SSTC for all macroplots (3135 g $m^{-2}yr^{-1}$) is greater than both figures. Hopkinson et al. (1978) studied production in seven marsh macrophytes in Louisiana by the Wiegert and Evans method. Mean production in pure stands of Salicornia virginica at Los Penasquitos (SSTC = 2789 g $m^{-2}yr^{-1}$) is nearly equal to that of Distichlis spicata; greater than Phragmites communis, Sagittaria falcata, Spartina alterniflora and Spartina cynosuroides; but less than half that of Spartina patens. That the high level of salt marsh production reported for low latitudes on the Atlantic Gulf Coasts is duplicated in southern California marshes supports the universality of a latitude-production gradient.

The Spartina Question

Spartina foliosa dominates low marsh environments from northern California (Humboldt Bay) to the southern most extent of salt marsh at Laguna Ojo de Liebre, Baja California (Phleger 1965, Macdonald 1967). A tall (1 m) rhizomatous grass with prominent aerenchyma tissue, Spartina foliosa is capable of withstanding long submergence (Purer 1942). Macdonald (1977) recognizes two distinct groups of estuaries and coastal lagoons in southern California based in part on the presence of this grass. The first of these is characterized by having deep channels, large tidal prism, perennial ocean contact and well-developed, pure stands of Spartina foliosa directly above mudflat. The second group includes those with insufficient tidal prism to prevent seasonal or long-term closure of their ocean inlets. Invariably, according to Macdonald (1977), Spartina foliosa is absent from the second group. The results of this investigation do, for the most part, support

Macdonald's observation; vigorous stands of Spartina foliosa were present at Newport and Sweetwater; Spartina foliosa was absent at Los Penasquitos. But, presumably, the tidal prism at Los Penasquitos was once greater for Purer (1942) reported not only the presence of Spartina foliosa there, but that it was more luxuriant than elsewhere, twice as tall, greener and stiffer and less subject to being matted and becoming blown down. The restricted distribution of Spartina foliosa at Mugu Lagoon where tidal fluctuation is reduced (Warme 1971), and its absence from diked marsh at La Ballona Creek (Clark 1979), lends further support to the Macdonald (1977) model. The occurrence of Spartina foliosa at Bolsa where tidal fluctuation has not been permitted since 1899 is, therefore, difficult to explain. Perhaps the unique environment created by artifical removal of tides is a factor. Yet, because the salinity regime and soil alkalinity at BB-3, 4, 5, where this grass was sampled were characteristic of sea water, and because elevations there were well below MHW, it is likely that some sea water inflow through the permeable beach sands occurred and thus permitted Spartina, which was probably present in the bay before 1899, to persist. The answer to this question, however, may never be known, for with the return of partial tidal fluctuation to Bolsa in November 1978, Spartina foliosa sites were drowned and the most plants deceased.

Effects of Longterm Removal of Tidal Access--Bolsa Bay

Vegetation and environmental measurements together suggest that the absence of tidal fluctuation for 80 years strongly influenced but did not totally alter the salt marsh system of Inner Bolsa Bay. Net production of vascular plants, except for Spartina at macroplot 5 which appeared to be dying out as the study progressed, is comparable to that observed elsewhere.

Negative redox potentials and attendant anaerobisis were among the more significant effects of diking and removal of the tides. Peat accumulations 15 to 20 cm thick in each macroplot indicated poor nutrient turnover and restricted nutrient contribution to the adjacent mudflat and channel. Yet, nitrogen, which has been shown to be a limiting factor in other salt marshes (Valiela et al. 1975) did not appear to be limiting during the sampling period at Bolsa or at the other three study sites.

Comparison of the vertical range of salt marsh vegetation at Inner Bolsa with that of Outer Bolsa and the other southern California salt marshes included in this study (Figure 13) identified what appears to be the major alteration resulting from the removal of tidal flucutation. Apparently, in the 80 year absence of periodic inundation, salt marsh plants abandoned positions at or above MHW and re-established at anomalously low elevations. Frankenia grandiflora, for example, was located over 1.0 m below its normal elevation and .25 m below the lowest Spartina foliosa or Salicornia virginica found elsewhere. Yet, this anomalous condition may not be due to the removal of tidal fluctuation alone but a combination of tidal removal and subsidence (resulting from oil or ground water withdrawls or both). Moffatt and Nichol (1971) studied bench mark levels for the time period 1933 to 1964 and estimated subsidence at between 23 and 46 cm. Orange County bench marks along the west side of Inner Bolsa have been repeatedly surveyed and show continued

loss of elevation. For example, bench mark IJ-29-68 near the sampling transect descended by 8.4 cm between 1968 and 1976. From the available data, a mean subsidence rate for Inner Bolsa may be estimated at about 1 cm per year.

Subsidence, then, could account for a marshland shift downward of approximately 80 cm since the removal of tidal fluctuation and, together with some re-establishment or vegetation extension of marsh plants to lower levels, may be responsible for the anomaly. Whatever the cause, however, it is obvious that restoration of unrestricted tidal access to Inner Bolsa (as with a new channel to the Pacific Ocean which is under consideration) will lead to prolonged inundation and destruction of some existing salt marsh.[1]

[1] Following the construction of a parking lot for visitors and a new dike to prevent inundation of land owned by Signal (Figure 5), partial tidal contact as mentioned above was returned to 52 ha of Inner Bolsa by removing flap valves on culverts through the old dike. The marsh is now (August 1979) in an advanced state of decay and, due to the restricted nature of the culverts, water fluctuation is limited to about .5 m above -.75 MHW.

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APPENDICES

Appendix A. Macroplot living and dead standing crop biomass (g m^{-2}).

Marsh	Macroplot	Living Biomass							Dead Biomass						
		Harvest Session							Harvest Session						
		1	2	3	4	5	6	7	1	2	3	4	5	6	7
SRE	1	1955	1377	680	1327	2093	1725	1379	829	971	789	2056	1752	1248	1374
	2	678	390	269	438	771	762	369	123	107	113	68	250	234	186
	3	682	1185	650	1189	1512	1565	1534	967	1945	1616	1250	2371	1558	1230
	4	555	1059	239	544	476	1136	754	114	574	297	622	593	700	641
	5	462	1023	215	337	486	968	867	860	643	386	712	990	904	525
	6	999	476	759	735	1313	1238	1211	700	1516	822	967	1518	780	1428
	7	365	619	236	344	739	529	1461	154	510	247	563	1190	655	1148
	8	489	566	181	705	1385	1095	1545	193	895	71	507	1458	987	895
	9	1737	525	446	709	777	688	526	505	438	406	300	807	636	446
	10	227	534	503	510	729	738	280	159	358	510	238	280	786	397
	11	702	980	599	619	1158	1150	980	690	845	544	669	1018	652	1106
	12	250	575	316	606	678	826	789	376	449	250	356	811	961	697
	13	1008	456	857	962	1[illegible]3	1391	921	667	915	771	757	1604	1496	1507
	14	995	401	149	318	470	496	831	88	969	1309	213	606	453	385
	15	188	85	47	195	204	293	376	157	297	167	72	164	326	232
	16	660	539	426	431	322	443	387	33	92	102	194	263	167	55
	17	845	1385	674	647	1186	173	1705	2097	1381	743	616	1301	1040	1435
	18	845	687	254	180	896	455	807	466	1230	701	706	1360	603	664
	19	715	973	894	1150	2840	2364	3430	2696	1548	2095	1269	1728	1159	2204
	20	527	778	865	1511	1193	914	910	545	297	631	461	678	562	401
	21	832	552	383	673	590	590	999	778	233	230	275	375	379	661
	22	1072	586	564	743	1169	963	1097	743	697	486	1039	941	1095	1183
	23	374	146	347	523	1419	1362	887	85	196	134	197	388	449	397
	24	736	297	608	579	1012	797	724	709	326	450	138	699	375	599
	25	218	900	333	1300	1902	1190	845	211	225	407	497	266	381	649
	26	185	78	174	810	629	723	322	0	147	181	206	285	267	246
	27	462	438	420	745	1094	1042	654	302	460	333	803	364	502	364

continued

Appendix A. cont.

Marsh	Macroplot	Living Biomass							Dead Biomass						
		Harvest Session							Harvest Session						
		1	2	3	4	5	6	7	1	2	3	4	5	6	7
SRE	28	861	349	417	602	824	563	631	261	472	383	1319	796	409	552
	29	45	455	99	553	474	233	120	198	300	111	378	186	478	153
	30	552	589	259	1033	579	515	831	221	363	102	643	439	137	448
	31	790	417	225	439	427	1023	1043	72	173	159	269	150	559	296
LPL	1	2564	960	1325	583	1623	2258	1180	1247	834	1481	466	514	532	607
	2	1164	1567	1127	722	1624	1744	1203	760	892	534	447	580	814	952
	3	989	2983	1459	1059	1471	1734	1738	858	830	634	176	68	185	523
	4	2509	1912	1421	514	1252	1467	1665	839	1017	560	243	1123	1110	743
	5	1390	---	1213	1317	1556	1578	1435	2838	---	2469	1156	1942	2780	1669
	6	831	2607	813	1991	2119	2308	2637	2786	2111	2566	2057	2634	3447	2079
	7	2880	1767	1269	1488	1158	1584	2434	839	1498	1557	1229	1091	1149	1281
	8	502	274	202	213	583	663	598	4183	4552	2696	2345	4543	4749	2872
	9	1181	853	467	654	1038	1625	1556	1940	2864	2133	1687	2049	2904	2556
	10	2323	1228	425	1041	1040	1082	2050	1091	1677	419	475	762	1012	646
	11	3303	1993	1548	2597	2965	2031	1858	806	836	1280	575	887	3713	2421
	12	1269	58	802	1067	920	574	484	2197	3336	2008	2507	2159	2010	2177
	13	45	10	0	24	0	1	21	1036	1508	845	1409	715	642	762
	14	1164	746	945	882	393	1199	538	1688	1137	1017	964	855	1329	1262
	15	3915	1931	1206	1898	1949	1787	946	1523	1901	856	1800	1458	1802	988
	16	1003	625	476	411	1750	1390	1292	1501	1620	487	917	484	1402	2134
	17	457	1306	1050	1180	353	808	599	1647	1603	1963	989	1367	1374	1675
	18	3238	3241	703	1242	1605	2225	1916	1272	1774	830	1965	770	1535	1445
	19	1308	718	780	1091	1061	1783	1684	1613	2860	1832	2142	1500	1383	2033
	20	1009	1256	1003	657	729	2391	1143	1303	1029	1353	1483	657	868	1416
	21	551	938	731	960	1018	1276	1214	1073	1043	824	597	798	1066	840
UNB	1	908	1023	414	569	1178	487	573	365	401	352	316	222	345	346
	2	636	418	325	762	922	587	552	486	412	304	331	656	219	313

continued

Appendix A. cont.

Marsh	Macroplot	Living Biomass							Dead Biomass						
		Harvest Session							Harvest Session						
		1	2	3	4	5	6	7	1	2	3	4	5	6	7
UNB	3	597	922	556	954	1231	1004	1056	236	491	254	403	533	329	352
	4	623	382	358	620	711	667	556	349	341	325	228	1075	561	574
	5	464	395	464	425	315	789	665	357	539	504	814	790	898	638
	6	854	221	139	288	503	294	756	502	966	834	1125	1049	895	683
	7	263	356	172	585	360	670	426	750	573	393	314	595	890	557
	8	553	538	297	919	1554	795	1070	162	586	171	770	762	656	469
	9	211	349	341	714	858	717	425	216	45	83	183	129	403	223
	10	878	355	315	629	769	948	467	554	364	342	405	944	929	737
	11	243	206	411	692	1177	814	420	147	96	106	114	456	243	271
	12	493	833	718	863	662	511	377	301	491	253	327	634	713	470
	13	1679	181	139	301	398	687	561	267	637	495	1134	1218	922	807
	14	292	546	318	624	973	808	889	454	389	227	239	230	48	260
	15	225	436	234	590	656	559	739	416	511	138	127	534	183	263
	16	15	50	82	385	524	347	421	334	207	116	204	98	36	145
	17	591	429	186	279	666	784	724	345	293	119	0	388	236	434
	18	645	423	327	1156	1035	860	1140	321	136	141	253	457	493	435
	19	257	175	94	310	520	425	212	72	196	92	171	92	142	243
	20	685	221	71	379	241	377	547	326	845	738	696	1195	856	784
	21	1075	449	481	447	369	683	593	473	354	331	501	558	367	304
	22	115	156	152	528	855	789	866	208	151	137	130	48	97	171
	23	728	604	210	544	191	813	339	1137	1184	625	1072	598	1440	865
	24	870	734	209	719	245	736	1294	570	417	145	917	355	985	1456
	25	614	266	104	457	338	295	349	610	958	322	694	1491	1194	998
BB	1	149	1633	642	956	2059	1563	1270	927	732	143	1088	1233	873	1467
	2	628	622	274	969	709	662	630	784	495	411	505	445	608	887
	3	598	349	135	817	639	474	519	1046	411	320	380	1083	938	1602
	4	423	28	4	61	37	203	0	1231	770	208	702	295	1096	578
	5	16	50	2	0	0	0	0	62	51	2	72	16	34	62

Appendix B. Net Production for Plant Species by Macroplots (g $m^{-2}y^{-1}$)

Site		Bama	Crtr	Cusa	Disp	Frgr	Juca	Lica	Losc	Moli	Coma	Sabi	Savi	Spfo	Suca	Trma
SRE	1					3445							131			
	2	137				342		88					998		121	103
	3	6				1357	1						3138		391	
	4	107				404	2	1					2167		130	
	5	175					504						1435			
	6					1147				43			1811		33	18
	7	68			47	422		10		49			2814		3	47
	8	209		238	4	1349		136		204		1	2218	15	82	80
	9	70				549		127		246			1804		7	99
	10	40			80	206		65		122			554		33	409
	11	221				504				550			1249			
	12	176				718		12		82			942		1	29
	13			2	315	542	10	575		562			892		43	67
	14													1824		
	15												620			
	16	81				12	284					366	517	5		57
	17				160	415	3						3732	3		
	18													2659		
	19					6231										
	20	955						320				4	1319		33	
	21	841						862				1	482		179	197
	22	980		28		698		245					1258		882	
	23	779			114							713	869			26
	24	420		18	99	34	263	208				55	926		168	7
	25	129			114		2395					272	153	345		
	26	3			15	5		1				632	156			792
	27	375			263		845	60				355	22	98	383	25
	28	28			1426	68	169	7				25	663		93	
	29	20				4		476				273	45			376
	30	95				24	381					458	1122	545		

continued

Appendix B. cont.

Site		Bama	Crtr	Cusa	Disp	Frgr	Juca	Lica	Losc	Moli	Coma	Sabi	Savi	Spfo	Suca	Trma
LPL	1												5011			
	2												2088			
	3												3155			
	4												3067			
	5					1831							1905			
	6					4864							574			
	7												2287			
	8		250		1184	2962										
	9					3175							1994			
	10												3056			
	11												5303			
	12		4			4240							1176			
	13												1767			
	14												2690			
	15												5848			
	16												3224			
	17												2047			
	18												5219			
	19				2574								1370			
	20												2417			
	21												1582			
UNB	1							357		1351						
	2	5				12		348		892	8		295		10	
	3	72			64	112	154	403		833			333		312	20
	4	222		1			414					1	216	790		31
	5	231					407						747	663		95
	6													1339		
	7				401				5	999						
	8	58			239	175	21	816		1182		1	443		142	85
	9	26			43	16	470	123				466	125			511

continued

Appendix B. cont.

Site		Bama	Crtr	Cusa	Disp	Frgr	Juca	Lica	Losc	Moli	Coma	Sabi	Savi	Spfo	Suca	Trma
	10	205			1561		94						44	52		235
	11	36			162	18	554	6				103	323	9		388
	12	75			780	27	96	3				1	799			261
	13													2621		
	14	620			33	491						149	1077			
	15	75				184				6		4	1048			
	16	185			27	40		13					579	98	25	
	17	509				34							340	387		
	18	437			202		203					74	1203	55		65
	19	7			13	51	151	61				40	179	49		334
	20	14					32						10	1320		
	21	43		5	77	4	198	97					923	382		325
	22	58			8	7	499	72				101	206	95		274
	23													3217		
	24	320											3160	50	16	
	25	320												1969		
BB	1				74	4564										
	2				1178								1120			
	3				1452	72							1525	262		
	4												459	1032		
	5													164		

Appendix C.1. Salinity of Substrate at 0 to 5 cm (ppt).

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	41	42			48	47	48	LPL	1		80	16	15	11	36	
	2	48	50		35	52	64	52		2		104	27	22	11	25	
	3	38	41	20		48	58	45		3		66	16	12	10		
	4	52	41		33	53	65	61		4		92	22		10	27	
	5	53	51		36	50	60	60		5	64	108	14		11		
	6	41	42	22	30	52	55	52		6		93	8	12	11	32	
	7	55	50		37	42	56	58		7	48	44	21	20	15	30	
	8	61	51			56	58	60		8			18				
	9	61	42			64	72	75		9			20				
	10	67	60		36	105	72	70		10		102	20		7	28	
	11	59	58			96	72	75		11		85	15		10	15	
	12	55	54			72	75			12					13		
	13	45	44	26		50	64			13	62	40	31	46	15	38	
	14	43	40	34	38	40	44	44		14		101		30	16		
	15	106	121	42		78	96	96		15		79	22	16	11	23	
	16	44	48	33		54	62	60		16		97	26	15	8		
	17	52	50	34		49	68	62		17		125		15	10		
	18	47	43	28	32	40	44	40		18	42	67	20	14	10	27	28
	19	48	38	25			62			19		102	14		12		
	20	41	44	28	48	54	62	53		20		94		16	13		
	21	48	50	27	38	62	68	60		21		115		29	10		
	22	43	40	24	42	60	57	49									
	23	47	44	35	50	46	58	55	UNB	1	44	15					41
	24	42	45	26	40	53	55	56		2	49	10	11		90		
	25	54	43	28	44	48	58	55		3	59	9	28	40	58	42	50
	26	60	45	28	45	46	60	60		4	39	26	23	37	46	46	43
	27	42	45	28	42	45	58	54		5	41	27	25	33	43	35	43
	28	41	45	31	42	56	60	56		6	35	20	24	30	37	40	41
	29	41	45	31	42	56	64	56		7		55					

continued

Appendix C.1. cont.

Marsh	Harvest Session							Marsh	Harvest Session						
	1	2	3	4	5	6	7		1	2	3	4	5	6	7
SRE 30	44	44	31	40	45	64	55	8	45	5	5	34	64	44	64
31	44	41	30	40	42	52	48	9	42	22	28	35	54	50	52
UNB 10	40	18	24	32	41	44	44	BB 1	22	7	10	7	20	28	45
11	47	22	24	37	48	50	41	2	30	10	13	13	30	34	36
12	40	22	22	34	60	50	47	3	37	29	16	27	35	48	38
13	38	29	37	36	42	38	37	4	38	33	34	35	48	45	44
14	60	44	34	64	77	76	70	5	39	33	27	47	54		44
15	55	44	34	55	82	85	81								
15	55	44	34	55	82	85	81								
16	55	43	35	56	83	91	83								
17	61	57	35	48	56	68	61								
18	45	41	31	42	61	51	48								
19	42	25	29	40	60	63	52								
20	37	37	31	35	40	40	38								
21	40	28	27		41	45	38								
22	41	26	24	40	52	51	47								
23	36	25	22	34	37	36	36								
24	40	27	30	34	40	49	42								
25	37	27	30	35	40	38	35								

Appendix C.2. Salinity of Substrate at 45 to 50 cm (ppt).

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	43	42			40	47	48	LPL	1	26	50	47			25	20
	2	52	53		45	44	49	60		2		60			25	25	
	3	49	53			42	50	51		3	40	50			21	25	12
	4	55	50	50		47	55	55		4		51	44		20		20
	5	55	50		49	48	47	48		5	39	70			21		25
	6	63	44			42	50	54		6		71	32		17		
	7	57	53	44		36	43	61		7	26	81	41	22	25	10	
	8	70	59	44		36	51	56		8		64					
	9	77	62	54	42	54	60	66		9							
	10	71	72			61	61			10		64					
	11	93	70			55	61	62		11		75	41				
	12	67	68		70	60	64			12							
	13	60	50			36	49	62		13	55	51		36	44	54	60
	14	54	42	42	35	38	40	40		14	56	55					
	15	95	102	102	98	82	104	105		15	24	55		14		28	22
	16	50	61	49	44	49	58	60		16		58				52	68
	17	53	40	47		39	60	55		17		66				55	62
	18	44	40		35	36	40	40		18	28	37	55				
	19	50	38	30	27	44	42	48		19		58					
	20	40	50	42	49	45	46	49		20		63				55	
	21	42	54	46	44	45	58	52		21		69				54	64
	22	50	50	35	45	42	48	52									
	23	58	48	53	36	49	51	61	UNB	1	52	37	3				48
	24	55	51	42	38	38	50	55		2	48	41	22		30	40	48
	25	45	48	41	40	42	62	55		3	44	36	21	25	32	36	45
	26	45	50	45	48	48	58	62		4	44	37	42	32	35	40	46
	27	46	53	37	42	40	53	56		5	43	36	32	30	32	39	40
	28	48	39	44	44	42	48	48		6	36	32	33	42	36	36	48

continued

Appendix C.2. cont.

Marsh	Harvest Session							Marsh	Harvest Session						
	1	2	3	4	5	6	7		1	2	3	4	5	6	7
SRE 29	60	48	39	42	43	57	58	7	49	32	4				50
30	48	46	36	42	38	62	54	8	54	39	18	27	22	43	34
31	42	42	37	40	32	41	42	9	49	37	34	32	48	59	55
UNB 10	40	37	34	32	33	42	44	BB 1	22	22	19	22		20	25
11	45	37	33		44	55	52	2		20	27	29	31	35	36
12	40	33	25	36	45	50	48	3	34	31	35	35	41	35	29
13	38	37	34		37	40	35	4	41	34	39	35	45	32	42
14	67	65	69			64	68	5	36	36	40	36	48	47	38
15	72	67	70		78	60	65								
16	63	65	63	62		66	60								
17	53	68	56			64	62								
18	51	52	46	45	44	48	44								
19	60	51	42	54		58	62								
20	38	38	39		40	34	30								
21	43	34	26			50	45								
22	44	41	40	32	40	43	46								
23	35	35	28	32	35	34	37								
24	38	35	36	32	36	40	48								
25	36	35	29	30	38	34									

Appendix C.3. Salinity of Substrate Free-water (ppt).

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	40	47	20		48	46	50	LPL	1	32	50	33	9			
	2	55	50	34	47	44	55	60		2		54	40	12	15		
	3	48	40	28		47	48	50		3	56	26	6	19	26		
	4	52	43	38		40	50	50		4		51	33	16	10	27	
	5	46	45	30	34	42	48	50		5		56	20	10	10	20	
	6	43	40	24			49	50		6		61	28	16	6		
	7	52	44	29		40	47	47		7		35	32	16	15	26	20
	8	54	50	36		45	58	60		8			24				
	9	62	45	42		54	65	66		9			29	25			
	10	57	61	26		60	68	62		10		54		16	15		65
	11	58	52	26			72	65		11		65	20	10	16	20	46
	12	61	54	37			70	54		12			31				
	13	35	40	22			47	52		13		51	35	5	10	55	62
	14	37	40	33		36	40	40		14		51	24	22	18	48	
	15	94	72	103				102		15	32	45	33	8	13	16	34
	16	48	48	44		47	54	58		16		54	41	28	16	60	70
	17	40	43			37				17	62	57	34	15	18	55	62
	18	38	37		31		40	40		18	25	35	23	3	25	16	
	19	45	37	27				42		19		55	28	25	20	25	
	20	55	44	27	38	51	54	52		20		54	26	12	17	52	
	21	55	45	31	38	50	58	60		21		61	32	8	22	60	
	22	50	39	28	42	40	48	50									
	23	50	44	30	35	45	57	60	UNB	1		3	3				34
	24	52	44	27	37	48	52	54		2	46	10	12			48	48
	25	52	42	30		45	55	56		3	39	14	18	23		44	48
	26	50	43	32		50	57	55		4	42	39	30	30		40	44
	27	50	43	30		43	54	52		5	42	36	25	28		38	42
	28	43	45	42		38	42	45		6	35	19	22	30	34	36	34
	29	48	43	30		46	53	50		7		5	3				

continued

Appendix C.3. cont.

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	30	50	40	38		46	54	52		8	40	24	11	11		45	
	31	42	37	30	34	40	40	42		9	45	39	32	32		50	52
UNB	10	38	33	25	26	35	38	40	BB	1	31	13	14	7	15	20	25
	11		34	28	30	50	38	44		2	37	9	16	18	29	30	32
	12	34	28	23	31		42			3	31	26	16	26	40	41	40
	13	35	23	22	32	34	34	34		4	37	26	25	35	48	45	47
	14	61	40	45	48		70	71		5	37	26	9	41	42	50	42
	15	70	57	44	50		78	74									
	16	70	46	61	56		68	65									
	17	65	56	40	44		60	65									
	18	49	44	37	46	45	46	50									
	19	41	39	36	34		50	62									
	20	41	30	27	34		35	28									
	21	38	27	22	32		36	42									
	22	40	30	22	35		48	45									
	23	33	30	23	28	41	34	34									
	24	37	28	22	28		38	38									
	25	36	33	21	25	31	35	30									

Appendix C.4. Reaction (pH) of Substrate Free-Water by Harvest Session (Assume One Decimal Place).

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	62	68	70		67	66	70	LPL	1		68	67	67			
	2	63	66	66	66	64	66	65		2		73	69	69	67		
	3	56	60	62		62	62	58		3		65	63	68	63	65	
	4	59	60	63		60	61	62		4		66	66	66	67	68	
	5	61	67	71	73	68	68	66		5		64	67	69	66	72	
	6	61	64	64			63	60		6		66	67	68	67		
	7	63	62	65		64	62	62		7		59	60	63	64	69	
	8	60	65	64		64	66	62		8		72					
	9	61	66	64		61	67	62		9			70	70			
	10	64	65	67				62		10		63	62	70	65		
	11	63	67	70			66	64		11		64	64	69	63	66	63
	12	69	68	67			66	64		12			70				
	13	69	65	72			62	64		13		68	67	70	72		
	14	63	69	65		65	65	63		14		67	67	68	61	70	
	15	64	76	67						15		64	63	63	66	68	
	16	70	60	61		61	61	59		16		70	65	68	64	67	76
	17	62	55			69				17	73	67	69	66	69	67	
	18	64	62		70		66	64		18		63	67	71	62	63	
	19	72	74	76			70	72		19		70	67	68	63	78	
	20	70	67	72	62	69	66	69		20		74	68	69	66		
	21	67	66	70	68	67	67	68		21		73	71	69	67	73	
	22	69	69	73	78	66	66	70									
	23	68	67	79	70	66	68	70	UNB	1		88	85				
	24	68	67	69		68	67	71		2	75	77	72			72	71
	25	65	60	69		66	65	68		3	74	74	72	69		70	
	26	63	61	64		63	61	63		4	63	61	64	62		61	62
	27	61	57	63		64	60	63		5	74	61	65	61		62	60
	28	60	59	59		60	58	60		6	67	65	66	63	68	66	65
	29	60	60	62		60	59	60		7		82	78				

continued

Appendix C.4. cont.

Marsh	Harvest Session							Marsh	Harvest Session						
	1	2	3	4	5	6	7		1	2	3	4	5	6	7
SRE 30	60	55	66		60	57	62	8	70	74	73	70		69	
31	63	59	66	69	65	67	64	9	62	63	64	67		62	62
UNB 10	62	62	63	61	68	59	70	BB 1	74	70	72	70	69	72	68
11		63	62	62		66		2	77	77	74	69	69	71	71
12	65	66	67	65		64		3	79	73	75	70	68	72	72
13	64	69	68	68	68	70	69	4	71	73	69	70	73	68	72
14	61	64	63	66		63	61	5	80	78	76	72	74	72	74
15	60	60	64	61		61	57								
16	60	60	62	61		62	65								
17	67	61	68	63		59	52								
18	57	57	62	55	59	60	57								
19	63	61	63	63		63	63								
20	67	66	67	66	69	65	72								
21	61	64	63	63		66	61								
22	61	63	62	61		62	68								
23	68	64	72	64		65	65								
24	61	64	75	80		64	62								
25	68	68	68	71	66	65	64								

Appendix C.5. Ammonia in Substrate Free-Water (10^{-5} M).

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	9		1		24	9	60	LPL	1		11	4	7			
	2	15		1	3	9	5	9		2		4	1	7	25		
	3	4		1		15	6	29		3		9	1	5	54	19	
	4	12	17	2		10	9	66		4		4	1	7	41	41	
	5	23		5	22	21	34	25		5		4	1	6	22	23	
	6	17		1			7	15		6		29	1	8	64		
	7	6	15	1		10		20		7		11	3	19	55	230	
	8	11		1		20	20	12		8			2				
	9	18		1		41	6	13		9			2	10			
	10	8		3			6	8		10		42	2	17	39		
	11	5		1			10	14		11		6	2	6	20	52	27
	12			2			9	14		12			1				
	13		13	3			7	10		13		10	4	20	54		
	14	36	11	1		11	5	20		14		2	3	6	18	18	
	15		13	2						15		1	2	8	24	35	
	16	15		1		11	15	7		16		6	3	5	39	33	
	17	24	14			18				17		8	3	5	41	42	
	18	10			11		12	16		18		10	2	5	25	42	
	19	36		1			10	6		19		1	1	5	43	22	
	20	30		1	24	11	6	23		20		1	3	6	28		
	21	30		1	9	4	5	7		21		3	6	6	380	28	
	22	24	14	1	15	8	4	9									
	23	60	10	1	4	5	6	9	UNB	1		7	3				
	24	60	10	1	15	4	4	5		2	21	2	8			8	6
	25	40	13	1		3	4	7		3	22	2	4	38		4	
	26	34	18	1		3	6	5		4	41	16	6	19		5	5
	27	34	18	1		3	9	6		5	16	32	3	12		17	6
	28	5	12	1		3	8	9		6	580	440	105	66	320	102	25

continued

Appendix C.5. cont.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
SRE	29	19	17	1		3	4	4
	30	7	17	1		3	3	7
	31	9	17	1	19	20	290	7
UNB	10	12	4	3	15	18	9	6
	11		7	4	9	16	26	
	12	24	3	3	18		36	
	13	105	42	26	132	360	640	77
	14	96	7	3	47		6	18
	15	45	12	15	55		8	20
	16	105	26	88	75		65	59
	17	100	3	210	134		35	6
	18	22	5	4	6	30	17	4
	19	11	4	3	56		20	8
	20	25	26	21	32	54	5	6
	21	26	5	7	19		7	3
	22	15	3	3	24		6	8
	23	108	8	13	33	130	66	26
	24	45	6	5	30		6	8
	25	120	13	6	14	54	49	87

Marsh		Harvest Session						
		1	2	3	4	5	6	7
	7		2	25				
	8	18	2	4	10		5	
	9	12	3	6	14		12	6
BB	1	43	30	15	8	42	24	67
	2	39	5	3	4	7	32	550
	3	72	3	3	6	10	56	94
	4	730	4	36	88	64	860	610
	5	75	6	11	78	17	690	95

Appendix C.6. Redox Potential (Eh·mV) for Substrate Free-Water.

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	1	407		382		497	422	367	LPL	1		427	312	307			
	2	447		427	367	492	417	447		2		437	357	352	262		
	3	317		357		482	427	407		3		442	302	412	272	252	
	4	297		407		427	427	247		4		437	292	402	232	282	
	5	372		407	317	442	397	407		5		367	292	422	237	289	
	6	412		377			427	442		6		337	322	417	327		
	7	387		397		467	397	432		7		437	282	352	182	347	377
	8	427		432		472	402	397		8			317				
	9	447		397		512	312	387		9			222	447			
	10	457		432				322		10		387	122	392	162		
	11	407		407			407	342		11		372	232	362	167	317	242
	12			427			417	342		12			337				
	13	392		407			412	427		13		407	342	392	227		
	14	247		297		462	317	392		14		327	332	407	272	187	
	15			427						15		327	312	417	187	247	
	16	392		367		482	417	302		16		397	237	372	257	237	347
	17	447				457				17	422	297	227	372	142	267	
	18	377			357		327	257		18	342	367	482	462	292	292	
	19	362		347			302	397		19		392	322	382	312	272	
	20	372		407	302	472	332	377		20		392	262	392	287		
	21	277		422	297	457	347	377		21		302	472	242	292	317	
	22	382		407	292	462	352	407									
	23	407		392	302	-18	367	347	UNB	1		422	382				
	24	447		422		467	372	392		2	342	357	337			387	247
	25	447		427		467	402	297		3	317	357	262	377		372	
	26	397		447		477	392	307		4	347	360	247	397		367	267
	27	397		442		477	87	347		5	262	364	187	397		177	397
	28	442		447		467	467	417		6	-78	382	82	407	-113	-43	-43

continued

Appendix C.6. cont.

Marsh		Harvest Session							Marsh		Harvest Session						
		1	2	3	4	5	6	7			1	2	3	4	5	6	7
SRE	29	327		447		472	387	427		7		512	127				
	30	432		442		472	387	402		8	297	462	337			412	
	31	197		307	257	472	352	359		9	197	392	362	387		259	292
UNB	10	337	537	337	357	217	367	297	BB	1	147	342	127	87	277	122	357
	11		472	327	447	277	217			2	212	289	22	137	57	42	322
	12	222	547	232	337		352			3	47	288	-33	37	27	-23	12
	13	-63	442	-98	-23	-73	-38	-98		4	-88	299	-126	-63	-43	-58	-73
	14	237	432	267	277		232	397		5	7	317	7	-53	-53	-78	-53
	15	227	392	357	397		357	267									
	16	272	338	182	407		357	367									
	17	177	381	-98	257		259	342									
	18	347	412	172	337	257	397	257									
	19	217	376	212	407		447	387									
	20	-38	417	11	397	147	357	262									
	21	137	362	167	347		377	367									
	22	192	422	197	397		382	337									
	23	67	384	237	297	97	47	72									
	24	212	382	247	267		422	287									
	25	-43	369	237	182	219	307	267									

Appendix C.7. Water Content (Percent) of Substrate at 0-5cm.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
SRE	1		52	39	33	38	39	37
	2	65	59	64	48	66	47	41
	3	57	63	58	46	42	48	38
	4	59	64	64	63	59	62	54
	5	56	53	53	56	53	54	47
	6	75	64	51	45	53	42	46
	7	56	47	50	40	54	52	30
	8	42	49	42		35	38	42
	9	48	49	44	38	42	35	37
	10	41	42	41	40	33	38	36
	11	41	42	43	43	37	33	39
	12	51	45	41	37	37	39	34
	13	47	39	40	30	31	35	33
	14		45		45	44	44	43
	15		38	31	27	25	28	31
	16	59	63	62	59	55	50	61
	17	41	41	44	37	46	42	40
	18	47	47	49	47	46	45	48
	19	38	43	32	40	30	31	37
	20	64	61	55	51	65	52	50
	21	51	48	49	48	58	49	61
	22		57	59	47	47	52	53
	23	66	64	69	63	69	68	45
	24	70	74	53	56	60	56	51
	25	54	64	64	69	66	66	65
	26	51	67	67	68	63	62	64
	27	64	61	65	61	63	41	61
	28	55	59	61	59	56	55	55
	29	56	59	57	58	58	56	55
	30	44	57	52	56	52	52	50
	31	50	42	40	41	41	44	38
LPL	1	49	41	63	63	69	57	33
	2	46	42	55	67	57	50	39
	3	47	45	61	55	55	56	41
	4	59	51	68	59	60	48	26
	5	49	48	53	54	62	51	38
	6	51	56	63	54	57	47	43
	7	51	57	57	61	61	55	52
	8	27	13	40	35	33	22	20
	9		28	41	33	34	20	17
	10		55	60	58	57	50	44
	11	54	55	58	66	66	61	49
	12	27	22	33	37	37	21	10

Marsh		Harvest Session						
		1	2	3	4	5	6	7
LPL	13	50	48	49	59	53	42	38
	14	40	41	52	51	50	41	35
	15	49	49	54	54	54	53	45
	16	35	40	51	54	51	39	31
	17	32	39	45	57	53	36	32
	18	50	45	55	55	55	50	44
	19	44	43	56	53	58	41	35
	20	32	34	50	55	47	35	28
	21	38	43	42	44	42	36	32
UNB	1	8	21	14	8	1	9	5
	2	15	21	20	18	11	19	11
	3	28	32	29	28	21	30	22
	4	69	72	75	72	69	69	71
	5	68	71	70	58	67	66	63
	6	65	68	68	67	65	68	62
	7		20	12	4	0	9	1
	8		29	32	25	19	30	22
	9		76	72	68	65	74	69
	10		73	65	71	67	66	64
	11		77	71	74	68	68	68
	12		57	53	64	43	53	45
	13		70	64	43	62	63	63
	14	69	74	71	43	68	71	69
	15	73	76	75	75	68	72	67
	16	75	76	76	75	69	70	69
	17	65	73	72	75	65	69	69
	18	72	77	80	78	72	77	78
	19	69	73	71	72	65	68	67
	20	69	68	69	70	71	72	68
	21	69	71	73	68	65	66	66
	22	63	66	67	66	62	62	66
	23	62	63	64	62	56	61	59
	24	52	58	48	57	47	51	44
	25	57	63	57	58	56	53	56
BB	1	42	50	37	78	64	46	51
	2	78	80	83	73	60	73	78
	3	85	86	89	77	86	85	86
	4	74	80	82		72	79	80
	5	76	65	82	89	79	75	77

Appendix C.8. Water Content (Percent) of Substrate at 45-50 cm.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
SRE	1		34	30	26	23	21	35
	2	45	48	47	47	47	48	53
	3	46	47	47	42	42	42	41
	4	48	62	51	40	56	47	29
	5	50	56	52	55	54	51	56
	6	30	34	37	40	30	31	32
	7	32	36	32	46	31	31	31
	8	30	30	31	20	28	29	56
	9	33	33	34	30	32	28	30
	10	32	31	31	27	29	28	28
	11	25	32	26	26	27	28	30
	12	27	26	27	25	24	27	24
	13	26	24	23	20	24	26	27
	14	34	38	26	54	38	40	40
	15		23	22	23	22	19	22
	16	35	35	32	32	34	37	36
	17	42	47	33	33	43	46	42
	18	47	45	47	47	47	44	57
	19		44	41	40	45	41	39
	20	56	57	59	57	56	56	54
	21	53	56	54	45	56	47	52
	22	49	50	50	49	49	48	47
	23	51	50	58	50	52	36	67
	24	53	52	65	36	35	29	37
	25	65	54	54	52	48	53	51
	26	68	55	47	53	49	48	51
	27	50	55	55	52	49	67	49
	28	32	54	52	50	54	51	50
	29	37	44	39	44	51	41	48
	30	50	38	45	40	44	38	45
	31	38	56	56	42	47	38	42
LPL	1	19		21	30	20	22	20
	2	19	17	19	22	21	25	19
	3	23	26	30	29	29	33	27
	4	27	37	36	45	31	35	31
	5	36	37	40	42	40	42	33
	6	22	38	27	38	32	35	32
	7	42	45	44	46	47	46	46
	8	15	19	19	23	22	17	12
	9		21	23	25	22	22	
	10	32		31	32	31	32	28

Marsh		Harvest Session						
		1	2	3	4	5	6	7
LPL	11	27	28	27	37	30	28	27
	12	27	28	31	25	27	28	25
	13	32	36	30	37	29	33	27
	14	29	30	18	33	34	28	29
	15	30	31	31	35	34	25	33
	16	28	28	27	31	30	30	27
	17	27	28	25	28	29	27	27
	18	40	40	40	43	42	39	40
	19	21	27	21	38	23	26	28
	20	22	29	27	28	30	45	29
	21	27	21	26	31	29	29	30
UNB	1	16	23	22	19	16	22	19
	2	25	23	25	25	23	36	23
	3	23	29	55	24	57	60	52
	4	46	45	48	59	47	44	30
	5	61	51	50	70	67	29	45
	6	52	56	54	54	52	55	55
	7		20	22	10	19	20	18
	8		32	65	25	56	62	61
	9		34	24	27	29	23	24
	10		29	26	31	25	30	22
	11		22	23	23	23	29	21
	12	23	27	33		21	23	20
	13		42	39	24	39	29	32
	14	40	22	23	22	31		43
	15	20	21	20	32	21	21	20
	16	57	21	29	39	21	22	20
	17	21	47		24	33	20	20
	18	35	38	34	36	26	29	25
	19	23	21	21	20	22	21	19
	20	22	26	26	30	23	24	24
	21	28	23	22	26	20	20	19
	22	44	42	39	45	34	30	35
	23	40	32	40	35	25	28	27
	24	51	56	46	54	39	43	54
	25	28	33	31	34	30	31	31
BB	1	23	25	27	28	23	24	22
	2	18	22	22	22	48	23	23
	3	39	36	20	23		21	36
	4	32	20	35	28	24	22	32
	5	37	19	25	21	23	41	42

Appendix C.9. Temperature (°C) of Substrate at 0-5 cm.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
SRE	1	21.5	16.5	11.7	15.0	17.2	17.8	16.7
	2	22.0	16.5	11.1	15.6	17.8	18.9	18.3
	3	21.5	17.0	11.1	15.0	17.8	18.3	17.2
	4	21.5	17.0	11.7	15.0	17.8	18.9	17.2
	5	22.5	17.5	11.1	15.0	18.3	19.4	17.8
	6	22.0	16.5	11.1	14.4	17.2	17.8	17.2
	7	21.5	16.5	11.1	15.6	17.8	18.9	17.8
	8	23.0	16.5	11.1	13.9	18.9	18.3	17.8
	9	22.0	16.5	11.1	14.4	21.1	19.4	18.9
	10	18.5	16.5	11.7	14.4	19.4	19.4	18.9
	11	22.0	16.0	11.1	14.4	18.3	18.9	17.8
	12	23.0	17.5	11.7	15.0	19.4	19.4	18.9
	13	21.5	16.5	11.7	14.4	18.3	17.2	17.8
	14	23.0	16.5	12.8	15.6	20.0	19.4	18.3
	15	23.3	17.0	12.2	16.7	23.3	22.8	20.0
	16	23.0	17.5	11.7	15.6	20.0	20.0	18.9
	17	23.5	16.5	11.7	14.4	18.3	19.4	16.7
	18	22.5	17.5	12.2	14.4	20.0	19.4	18.3
	19	22.5	16.5	11.7	13.9	16.7	17.2	17.2
	20	23.0	16.5	11.1	15.0	17.8	18.3	17.8
	21	22.5	16.5	12.2	13.9	18.3	19.4	20.0
	22	21.5	15.5	11.7	13.9	17.8	18.9	17.8
	23	21.5	16.0	12.2	14.4	18.9	19.4	18.9
	24	22.5	16.5	11.7	14.4	18.3	18.9	18.9
	25	22.5	16.5	11.7	13.9	18.3	18.9	18.3
	26	23.5	16.5	12.8	15.6	19.4	20.0	20.0
	27	22.5	16.5	12.8	14.4	18.9	18.9	18.9
	28	22.0	16.5	12.2	14.4	17.8	18.9	18.3
	29	23.0	17.0	12.8	16.7	20.0	21.1	20.6
	30	21.5	16.5	11.7	14.4	18.9	20.6	18.9
	31	22.0	17.5	12.2	16.7	20.6	21.1	20.0
LPL	1	19.5	13.9	11.1	13.9	18.9	17.8	17.2
	2	18.5	13.3	11.1	13.9	16.7	17.8	16.1
	3	18.5	13.3	10.6	15.0	18.1	17.8	17.2
	4	18.5	13.3	11.1	13.9	17.0	19.4	18.3
	5	18.5	12.8	10.6	13.3	16.1	16.9	16.1
	6	18.5	13.3	10.6	13.3	15.9	16.7	15.0
	7	18.2	13.3	11.1	14.4	17.0	17.5	14.4
	8		13.3	11.1	13.9	17.5	17.2	14.4
	9	18.0	13.9	10.6	13.9	17.2	17.8	17.2
	10	18.0	14.4	11.1	14.4	17.2	18.3	16.7

continued

Appendix C.9. cont.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
LPL	11	18.0	14.4	11.1	14.4	17.2	18.3	16.7
	12	18.0	10.6	12.2	14.4	18.9	20.0	20.6
	13	16.5	8.9	12.8	15.6	18.9	22.2	18.3
	14	17.5	9.4	11.1	13.3	17.2	19.1	16.1
	15	16.5	9.4	11.7	13.3	17.2	17.5	13.9
	16	17.5	12.8	10.0	13.9	17.8	20.9	16.7
	17	17.5	11.1	9.4	13.3	17.8	20.9	15.6
	18	17.0	11.1	8.3	12.2	18.3	18.9	14.4
	19	17.5	11.1	11.1	13.3	19.4	18.0	14.4
	20	17.0	10.0	11.1	13.9	18.3	19.4	16.1
	21	17.0	10.0	9.4	14.4	18.3	17.8	14.4
UNB	1	22.0	13.3	11.7	13.9	22.2	19.4	19.4
	2	20.0	12.2	11.7	13.9	20.0	20.3	17.2
	3	20.0	12.8	11.7	13.9	20.0	19.7	17.2
	4	20.0	13.3	12.8	14.7	18.9	18.0	17.2
	5	19.0	12.8	12.2	15.3	18.9	19.4	16.7
	6	19.0	13.3	13.3	15.3	19.4	19.7	16.7
	7	19.0	12.2	11.7	15.0	20.6	23.3	27.8
	8	18.0	12.8	11.7	13.3	17.8	17.8	17.2
	9	19.0	12.2	12.2	14.4	18.3	19.2	18.3
	10	18.0	12.2	11.7	13.9	17.2	16.7	16.1
	11	21.0	13.9	13.9	14.4	18.3	17.8	17.2
	12	19.0	14.4	13.9	14.7	18.3	17.8	15.6
	13	19.0	13.9	13.3	15.6	19.4	20.0	17.2
	14	22.5	12.2	13.3	15.0	20.6	19.4	16.7
	15	22.0	12.2	12.8	14.4	20.6	20.6	17.2
	16	22.5	11.7	14.4	15.6	19.4	21.7	18.3
	17	20.5	12.8	13.9	16.1	19.4	20.3	17.8
	18	18.5	11.7	14.4	14.4	18.9	17.8	17.2
	19	23.0	12.2	13.3	16.1	22.8	18.9	17.2
	20	18.5	12.8	13.9	16.1	21.7	17.5	17.2
	21	19.0	12.2	12.8	14.4	20.9	17.8	16.7
	22	19.5	12.8	13.9	16.1	20.6	18.0	16.7
	23	17.5	13.3	13.9	15.0	19.4	17.5	16.1
	24	18.0	12.2	12.8	14.4	20.0	16.7	15.6
	25	18.5	13.3	14.4	15.0	20.0	16.7	16.1
BB	1	14.5	12.2	12.2	15.0	17.2	17.2	17.2
	2	14.0	11.7	12.2	15.0	16.7	16.9	17.2
	3	15.0	12.8	12.8	18.9	17.8	17.8	17.8
	4	17.0	13.3	13.9	16.7	18.9	18.9	19.4
	5	15.5	13.9	14.4	20.0	20.0	18.3	20.0

Appendix C.10. Temperature (°C) of Substrate at 45-50 cm.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
SRE	1	18.9	13.9	12.8	13.9	16.7	17.2	17.8
	2	19.4	13.9	13.3	15.0	17.2	18.3	18.9
	3	19.4	13.9	12.8	14.4	17.2	16.7	17.8
	4	19.4	13.9	12.8	14.4	17.8	18.3	18.9
	5	19.4	15.0	12.8	11.4	17.8	17.2	18.3
	6	19.4	14.7	12.8	13.9	17.2	16.1	17.2
	7	19.4	14.7	12.8	14.4	17.8	17.8	18.9
	8	18.9	14.7	12.8	14.4	18.3	18.3	18.3
	9	19.4	14.7	12.8	14.4	17.8	18.3	18.9
	10	19.4	14.7	12.8	15.0	18.3	18.9	18.9
	11	19.4	14.7	12.2	14.4	17.2	18.3	18.3
	12	20.0	15.0	12.8	15.0	18.3	18.9	19.4
	13	20.0	15.0	12.8	14.4	17.2	17.8	17.8
	14	20.0	15.6	13.9	16.1	18.9	18.9	18.9
	15	20.6	15.3	12.8	16.7	23.3	22.2	20.6
	16	20.6	15.3	13.3	15.0	18.3	18.3	18.3
	17	19.4	15.0	12.8	15.0	17.2	18.3	18.3
	18	20.0	15.6	13.9	15.6	17.8	17.8	18.3
	19	19.4	13.9	12.8	13.3	15.0	15.6	17.2
	20	19.4	13.9	12.8	13.3	15.0	15.6	17.2
	21	20.0	14.4	12.8	15.0	17.2	16.7	17.2
	22	19.4	14.4	12.8	14.4	16.7	16.7	17.8
	23	19.4	13.9	13.3	15.0	17.8	18.3	18.9
	24	19.4	14.4	12.8	15.0	17.8	17.2	18.3
	25	20.0	14.4	13.3	13.9	17.2	17.8	17.8
	26	20.6	15.6	13.9	15.6	18.3	18.3	20.0
	27	20.0	13.9	13.3	15.6	17.8	17.8	18.3
	28	19.4	14.4	13.3	14.4	17.2	17.8	18.3
	29	21.1	15.6	13.9	16.7	18.3	18.9	20.0
	30	20.6	15.0	13.9	15.6	19.4	18.9	19.4
LPL	1	17.8	13.9	12.2	13.9	18.3	16.9	17.2
	2	16.7	13.0	11.7	13.9	17.0	16.9	16.7
	3	17.8	14.4	12.8	15.0	17.5	17.5	16.7
	4	17.8	13.9	12.2	13.9	16.7	16.7	15.6
	5	17.8	13.9	12.2	13.3	16.1	15.6	15.6
	6	17.8	14.4	12.2	13.3	16.1	15.6	15.6
	7	17.2	13.9	12.2	13.9	17.2	17.2	16.1
	8		14.4	11.7	13.9	16.7	17.0	16.7
	9	18.3	13.3	11.7	13.9	16.7	17.0	16.7
	10	16.7	13.9	12.8	13.9	17.0	16.9	16.7
	11	16.7	13.9	12.8	14.4	18.1	17.2	17.2

continued

Appendix C.10. cont.

Marsh		Harvest Session						
		1	2	3	4	5	6	7
LPL	12	16.7	13.3	12.2	15.0	17.8		17.8
	13	17.8	12.8	12.8	15.0	18.9	18.6	17.8
	14	17.2	12.2	12.2	13.9	17.2	17.8	16.7
	15	17.8	12.8	12.2	13.9	18.9	16.7	16.7
	16	17.2	12.8	12.8	14.4	17.8	17.8	18.3
	17	16.7	12.2	12.2	13.9	17.2	17.8	16.7
	18	16.7	12.2	11.7	13.3	17.2	17.0	17.2
	19	17.2	12.8	11.7	13.9	17.8	16.7	16.1
	20	16.7	11.7	11.7	13.3	17.2	17.8	17.2
	21	17.8	12.2	11.7	13.9	16.7	16.7	16.1
UNB	1	18.3	19.8	12.8	15.0	19.4	18.3	17.8
	2	16.7	12.2	12.2	15.0	19.4	18.0	17.2
	3	16.7	13.9	12.8	14.4	17.2	17.8	17.2
	4	16.7	13.9	12.8	14.7	17.8	17.5	17.2
	5	16.7	13.9	12.8	15.0	17.0	17.2	17.2
	6	16.7	13.3	13.3	15.0	18.9	17.8	16.7
	7	18.3	12.8	12.2	15.6	20.6	19.7	18.9
	8	16.7	12.2	12.2	15.0	18.3	17.8	17.2
	9	17.8	13.3	12.8	15.0	17.8	18.0	18.3
	10	16.1	12.8	12.2	13.9	17.2	16.4	16.1
	11	16.1	12.8	12.2	13.9	17.2	16.4	16.1
	12	16.7	13.3	12.8	14.4	18.3	16.9	16.7
	13	16.7	13.9	13.3	15.3	18.3	17.8	17.2
	14	17.8	13.9	13.3	15.6	18.9	18.3	18.3
	15	17.8	13.9	13.3	16.1	20.0	19.2	18.3
	16	17.8	13.9	12.8	16.1	20.0	19.2	18.9
	17	17.8	13.9	13.3	16.7	19.4	19.7	18.3
	18	17.2	13.3	13.9	15.0	17.2	17.2	17.2
	19	17.8	13.3	12.8	15.6	18.9	18.9	18.3
	20	17.8	13.9	13.9	15.6	18.9	17.5	17.2
	21	17.9	13.3	13.3	15.0	18.3	17.8	17.2
	22	16.7	13.9	13.9	15.6	18.3	17.8	17.2
	23	16.7	14.4	13.9	15.0	17.8	17.2	16.7
	24	16.7	14.4	13.3	13.9	17.2	16.9	16.7
	25	16.7	14.4	13.9	15.0	17.8	16.9	16.7
BB	1	14.4	12.8	12.2	14.4	17.2	17.2	17.2
	2	14.4	12.8	12.8	14.4	17.2	16.7	16.7
	3	15.6	13.9	13.3	15.0	17.2	17.2	17.2
	4	16.7	14.4	13.9	15.6	18.9	18.0	18.9
	5	17.8	14.4	15.0	16.1	18.9	18.3	18.9

Appendix D. Macroplot Elevation and Habitat Type. Habitat as Follows: Fore Levee Slope (1), Levee Crest (2), Back Levee Slope (3), Back Levee Depression (4), Slope Below Upland (5), Upland Transition (6), Pan (7).

Marsh		Elevation	Habitat
SRE	1	.34[a]	6
	2	.15	4
	3	.35	2
	4	.42	2
	5	.08	2
	6	.33	2
	7	.22	4
	8	.39	3
	9	.34	3
	10	.38	3
	11	.37	3
	12	.35	3
	13	.49	2
	14	-.30	1
	15	.52	7
	16	.13	4
	17	.33	2
	18	-.27	1
	19	.61	6
	20	.27	5
	21	.33	5
	22	.41	5
	23	.20	4
	24	.24	4
	25	.18	4
	26	.15	4
	27	.11	3
	28	.14	3
	29	.14	4
	30	.11	3
	31	-.17	1
LPL	1	.17	3
	2	.19	3
	3	.08	3
	4	.17	3
	5	.22	3
	6	.28	3
	7	.25	2
	8	.59	6
	9	.57	6
	10	.24	6
	11	.24	2
LPL	12	.51	6
	13	.21	1
	14	.29	3
	15	.27	2
	16	.15	4
	17	.17	4
	.8	.31	2
	19	.33	2
	20	.25	3
	21	.25	3
UNB	1	1.05	6
	2	.84	5
	3	.69	5
	4	.44	1
	5	.40	1
	6	.27	1
	7	1.17	6
	8	.77	5
	9	.51	3
	10	.47	3
	11	.49	3
	12	.55	2
	13	.18	1
	14	.70	4
	15	.70	4
	16	.70	4
	17	.62	4
	18	.65	4
	19	.59	4
	20	.33	1
	21	.56	4
	22	.54	3
	23	.31	3
	24	.53	2
	25	.22	1
BB	1	-.57	6
	2	-.87	5
	3	-.96	5
	4	-1.07	1
	5	-1.12	1

[a]Meters; reference is local MHW.